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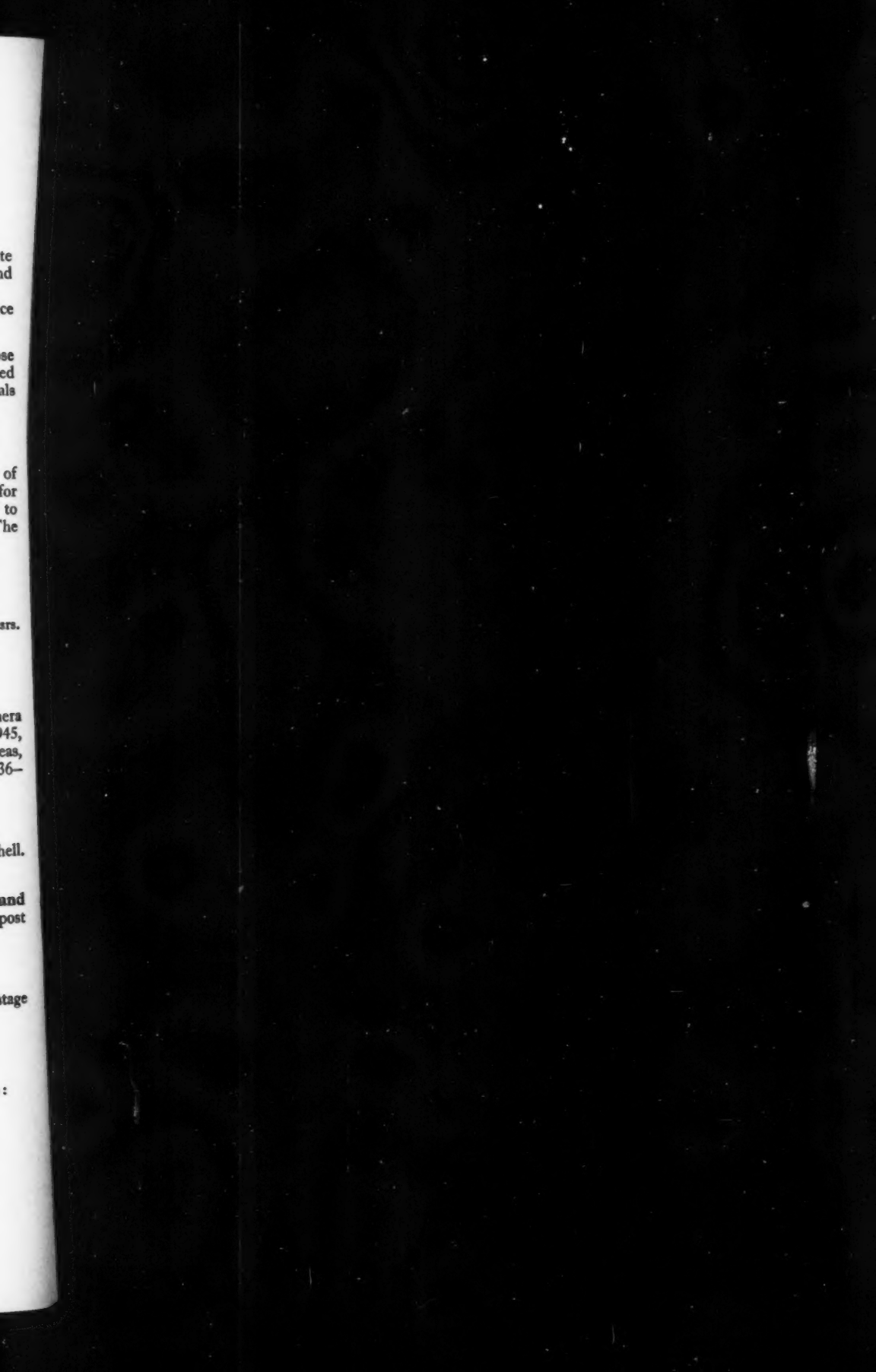


FURTHER CONTRIBUTIONS ON THE BUCCAL AND PHARYNGEAL MUCOUS MEMBRANE IN URODELES

BY

E. ELKAN, M.D., L.R.C.P.

Pinner, Middlesex.

[Accepted 11th February, 1958]

(With 2 plates and 12 figures in the text)

CONTENTS

	Page
Introduction	335
Material	336
Histology of mucous membrane	336
Schistometopum thomensis	338
Triturus cristatus	339
Triturus marmoratus	340
Salamandra salamandra	341
Euproctus asper	342
Euproctus montanus	343
Pleurodeles waltli	343
Ambystoma tigrinum	344
Amphiuma means	346
Batrachoseps attenuatus	347
Ensatina eschscholtzi	347
Plethodon glutinosus	349
Pseudotriton ruber ruber	350
Desmognathus ochrophaeus	352
Proteus anguineus	353
Conclusion	354
Acknowledgments	354
References	355

INTRODUCTION

In a previous paper (Elkan, 1955) endeavour was made to establish a relation between the histological anatomy of the oral mucosa and the respiratory habits in certain urodeles. By reason of the fact that many of the animals required were not readily available, the investigation could not be carried out systematically. Since then, more material having become accessible, a further number of species have been examined, and are dealt with in this paper. It has not been possible to deal with the Hynobiidae nor the Cryptobranchidae.

MATERIAL

The following species have been examined.

In 1955	In this paper
	A. Apoda
	Schistometopum thomensis Bocage
	B. Urodela
	1. Salamandridae
Triturus vulgaris Lin.	*Triturus cristatus* Laur.
Salamandrina perspicillata Bon.	*Triturus marmoratus* Latr.
	Salamandra salamandra Linn.
	Euproctus asper Dugès
	Euproctus montanus Savi
	Pleurodeles waltli Mich.
	2. Ambystomatidae
	Ambystoma tigrinum Green (larval)
	3. Amphiumidae
	Amphiuma means Gard.
	4. Plethodontidae
Aneides ferreus Cope	*Batrachoseps attenuatus* Eschsch.
Aneides flavipunctatus Str.	*Ensatina Eschscholtzi* Gray
Aneides lugubris Hallow.	*Plethodon glutinosus* Green
Desmognathus fuscus Raf.	*Pseudotriton ruber* Tschudi
Eurycea bislineata Green	*Desmognathus ochrophaeus* Cope
Hydromantes genei Schlegel	
	C. Proteidae
	Proteus anguineus Laur.

The available material is presented in the order of this list.

HISTOLOGY OF MUCOUS MEMBRANE

To facilitate orientation, the diagram, dividing the oral mucosa into eight different regions, is again reproduced (Fig. 1). It will be seen that even among closely allied species remarkable differences exist in the microscopical anatomy of the oral mucosa and that, with a few surprising exceptions, this organ shows no adaptation whatever that might be interpreted as facilitating gas exchange. There has, so far, been no opportunity to extend this investigation to the larval stage where, as Bruner (1914) and Whipple (1925) have shown, a current of water is aspirated through the nares and/or through the mouth and expelled through the gill slits. It is during this phase that the mechanism of gular vibration establishes itself but the fact that adult urodeles can be easily observed inserting long intervals in their gular activity when they are undisturbed, shows that in the adult this motion is no longer essential for the purpose of gas exchange. The body surface which, in all urodeles is considerable in relation to their weight, is sufficient to effect the necessary gas exchange, although anatomically the skin is no more adapted as a breathing membrane than the oral mucosa. But, as Bruner (1914) rightly stated, while the urodeles reduced or even lost their lungs, they did not at the same time loose or reduce their olfactory organs. Both the nasal capsule and the olfactory cerebral lobe are well developed, indicating the importance of this organ for the life of the animal. It is therefore not surprising that the gular vibrations, estab-

lished during early larval development, should later on be maintained for the purpose of ventilating the olfactory organ. All living urodeles are light-shy and are most active at night when their power of sight, which is poorly developed, is not vital to their activities. Observation on salamanders indicates that the role of the eye is to draw the animal's attention to a moving object. Further and closer inspection then takes place by bringing the nostrils as close to the object as possible, ventilating the nasal cavity vigorously all the time by way of gular movements. Once the animal has settled down to rest again and feels perfectly undisturbed, the gular movement may cease. The slightest disturbance however acts as a trigger to set it off again.

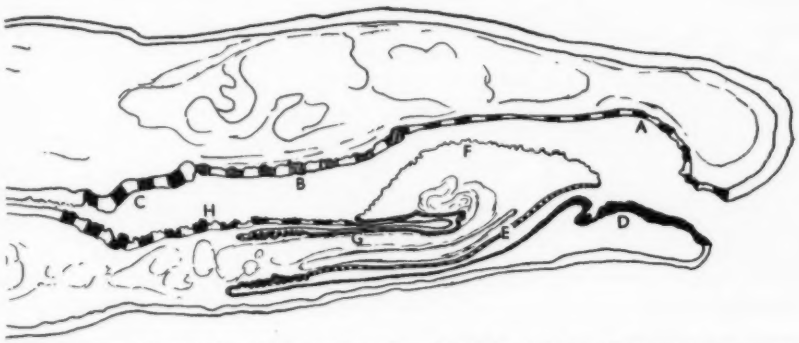


Fig. 1.—Diagram of sagittal mid-line section through the head of a plethodontid salamander, indicating the areas of the buccal and pharyngeal mucous membranes referred to in the text.

	Regions	
		Dorsal
A	Labio-nasal	From the maxillary teeth to the first sphenoidal teeth.
B	Sphenoidal	From the first to the last sphenoidal tooth.
C	Spheno-oesophageal	From the last sphenoidal tooth to the beginning of the oesophagus.
		Ventral
D	Mandibular	From the mandibular symphysis to the root of the tongue stalk.
E	Ventro-lingual, anterior	From the root of the tongue stalk along the anterior inferior surface of the tongue to the anterior tip of the tongue.
F	Dorso-lingual	Surface of the tongue from the anterior to the posterior tip.
G	Ventro-lingual, posterior	From the posterior tip of the tongue, along the posterior inferior surface of the tongue to the root of the tongue stalk.
H	Laryngeal	From the root of the tongue stalk to the beginning of the oesophagus.

SCHISTOMETOPUM THOMENSIS Bocage

Region A (Naso-labial)	Gradual transition from epidermis to cuboidal oral mucosa of varying thickness (3–10 cells). The epithelium is non-ciliated. Most conspicuous are large blood-filled subepithelial sinuses and numerous sub-epithelial capillaries along the antero-ventral aspect of the nasal cavity. These sinuses only extend as far back as the choana. At the entrance to the choana some sinuses are seen to extend into the epithelium.
Region B (Sphenoidal)	The epithelium is 3–5 cells thick and much more uniform in thickness than in Region A. There are many sub-epithelial but no intra-epithelial capillaries. The epithelium is non-ciliated.
Region C (Spheno-Oesophageal)	Non-ciliated, cuboidal epithelium, 2–3 cells thick. Sub-epithelial capillaries.
Region D (Mandibular)	Non-ciliated cuboidal epithelium of very varying thickness. Large goblet cells in the area which faces the ventral surface of the tongue. Large sub-epithelial blood-filled sinuses.
Region E (Ventro-lingual, anterior)	Thin, non-ciliated epithelium. Small goblet cells. Large blood-filled sinuses in the substance of the tongue.
Region F (Dorso-lingual)	Non-ciliated epithelium, 5–10 cells deep. Some mucous glands. No blood sinuses near the surface of the tongue.
Region G (Ventro-lingual, posterior)	There is no posterior ventro-lingual fold.
Region H (Laryngeal)	Sudden transition to thin epithelium of 1–2 cells depth. No ciliation. Small goblet cells. Few sub-epithelial capillaries.

General remarks

The outstanding feature in the histological anatomy of this species is the presence of large, blood-filled sinuses both in the anterior maxillary as in the anterior mandibular region. It is not thought that sinuses of this size which are comparable with those found in the feet of some species of *Aneides*, tend to increase the process of gas exchange. They must, firstly, slow down the rate of circulation ; they also must reduce the amount of blood which may come near the surface. The surface itself, i.e. the oro-pharyngeal mucosa, would certainly allow for a certain diffusion of oxygen and carbon dioxide but seems in no way specially adapted for the purpose.

The only other amphibian in which similar large venous sinuses have been found is *Amphiuma* a genus otherwise far distant from the coecilians. Whatever the function of these various venous reservoirs may be, it is most unlikely that they help or are in any way connected with respiration.

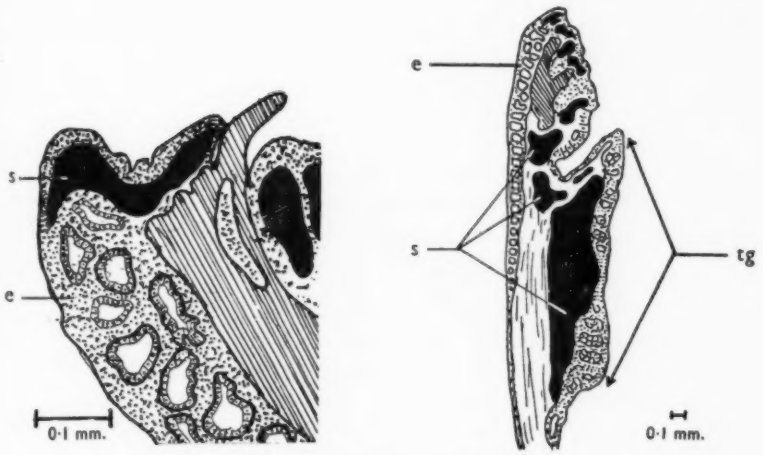


Fig. 2.—*Schistometopum thomensis*. Sagittal sections through lower jaw. Large, blood-filled sinuses are found throughout the head, some situated deeply, some intraepithelially. Like similar sinuses found in the feet of *Aneides lugubris*, these sinuses do not suggest that they assist in gas exchange. Their true function is as yet unknown. e. Epidermis ; s. Blood sinus ; tg. Tongue.

(Note : All line drawings illustrating this paper were executed by micro-projection).

TRITURUS CRISTATUS Laurenti

Site A (Labio-nasal)	Mucosa differs from epidermis only in the absence of the Stratum corneum. Depth of epithelium increasing from 3–4 to 4–7. No ciliation. No epithelial capillaries. Some large goblet cells present.
Site B (Sphenoidal)	Depth of epithelium 3–5 ; Ciliation present. No epithelial capillaries. Some capillaries at the base of the epithelium.
Site C (Spheno-oesophageal)	Epithelium looser in structure and more folded. Depth 15–20 cells. Ciliation present. Few capillaries at base of epithelium.
Site D (Mandibular)	Deep odontigerous pockets in the alveolar process. Epithelium folded with capillaries in the stroma. Some large goblet cells.
Site E (Ventro-lingual ant.)	Depth of epithelium 3–4. No ciliation. Some goblet cells.
Site F (Dorso-lingual)	Deep mucous glands lined with large goblet cells. No ciliation. Capillaries at base of epithelium. Lymphoid follicles in the epithelium.
Site G (Ventro-lingual, post.)	No posterior ventro-lingual fold present.
Site H (Laryngeal)	Epithelial loose in structure and more folded. Depth 5–10 cells. Ciliation present.

General remarks

Triturus cristatus has well developed lungs which, in a species of partly aquatic habits, probably act more as hydrostatic bags than as organs of gas exchange. The histology of the oral mucosa does not indicate that it participates in this function.

TRITURUS MARMORATUS Latreille

Site A (Labio-nasal)	The oral mucosa differs little from the epidermis. The depth of the epithelial lining gradually increases from 3–4 to 8–10. Some intraepithelial capillaries are present. There is no ciliation.
Site B (Sphenoidal)	Depth of epithelium 6–8. Capillaries only at the base of the epithelium. Ciliation present.
Site C (Spheno-oesophageal)	Depth of epithelium increases to 16–20. Capillaries only at the base. No ciliation.
Site D (Mandibular)	Depth of epithelium 4–6, increasing to 10–12. ciliated. Capillaries only at the base of the epithelium.
Site E (Ventro-lingual, ant.)	Epithelium folded, 4–10 cells deep. Goblet cells present. Capillaries in the stroma of the folds only.
Site F (Dorso-lingual)	Deep mucous glands lined with goblet cells. No ciliation. Capillaries at the base of the epithelium only.
Site G (Ventro-lingual post.)	Depth of epithelium 2–4 cells. No ciliation.
Site H (Laryngeal)	Depth of epithelium 5–7. No goblet cells. Ciliation present. Capillaries at the base of the epithelium.

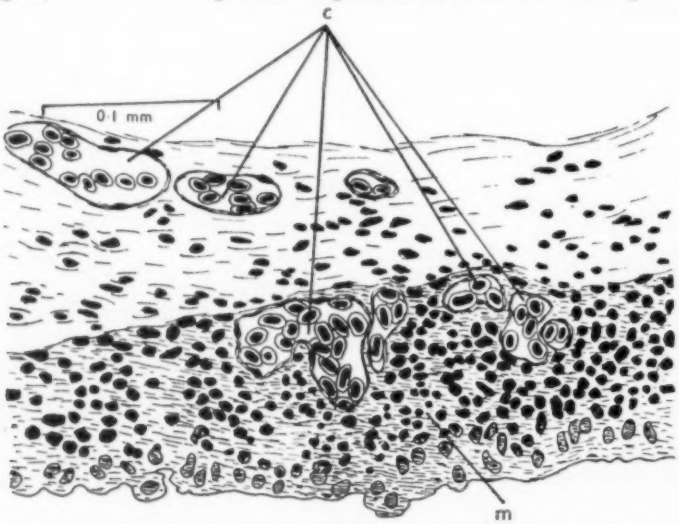


Fig. 3.—*Triturus marmoratus*. Region B. c, capillaries; m, mucosa.

General remarks

Where the oral mucosa reaches a thickness of over six cells depth, capillary loops are occasionally seen to penetrate the base of the epithelial layer (Fig. 3). These vessels are however not intraepithelial capillaries in the true sense and their function can be assumed to be nutritional.

SALAMANDRA SALAMANDRA Linné

Site A (Labio-nasal)	Sudden transition from external epidermis to oral mucosa at the alveolar process. High, ciliated columnar epithelium, 4–8 cells deep.
Site B (Sphenoidal)	Mucosa reduced to a depth of 3–4, ciliated. Capillaries at the border of dermis and epithelium.
Site C (Spheno-oesophageal)	Ciliated mucosa, cuboidal, 6–8 cells deep. Many capillaries at the base of the mucosa. Mucosal folds at the entrance to the oesophagus.
Site D (Mandibular)	Mucosa 8–12 cells thick, much folded. Some goblet cells, surface ciliated. Fewer capillaries at the base of the epithelium.
Site E (Ventro-lingual, ant.)	Mucosa 1–3 cells deep, gradually changing to a depth of 3–6 ciliated cells. Some goblet cells. No intraepithelial capillaries.
Site F (Dorso-lingual)	Deep crypts, lined with goblet cells. No ciliation. Capillaries in the stroma of the mucous glands.
Site G (Ventro-lingual post.)	There is no ventro-lingual fold. Ciliation recommences at the posterior end of the tongue. Mucosa gradually reduced to a depth of 3–4. Some goblet cells.
Site H (Laryngeal)	Thick mucosal folds (4–8) at the entrance to the oesophagus. Capillaries at the base of the ciliated mucosa. Many large goblet cells.

General remarks

While in some urodeles the difference between the epidermis and the oral mucosa is only slight, it is very marked in *Salamandra salamandra* (Fig. 4 A, B). In fact the columnar epithelium of the oral mucosa is so high and the capillary network at the epithelial base so developed as to distinguish *Salamandra* on sight from any other amphibian species. Yet these capillaries all lie at the border between dermis and epithelium and are separated from the surface by a layer of very long mucus-filled goblet cells. In spite of their marked development they cannot, therefore, be called "intraepithelial" and their function must be regarded as nutritional, not respiratory. This the more so since *Salamandra*, a very sluggish and retiring animal, has not only lungs but a dermal capillary network under the skin as well. (Pl. 1).

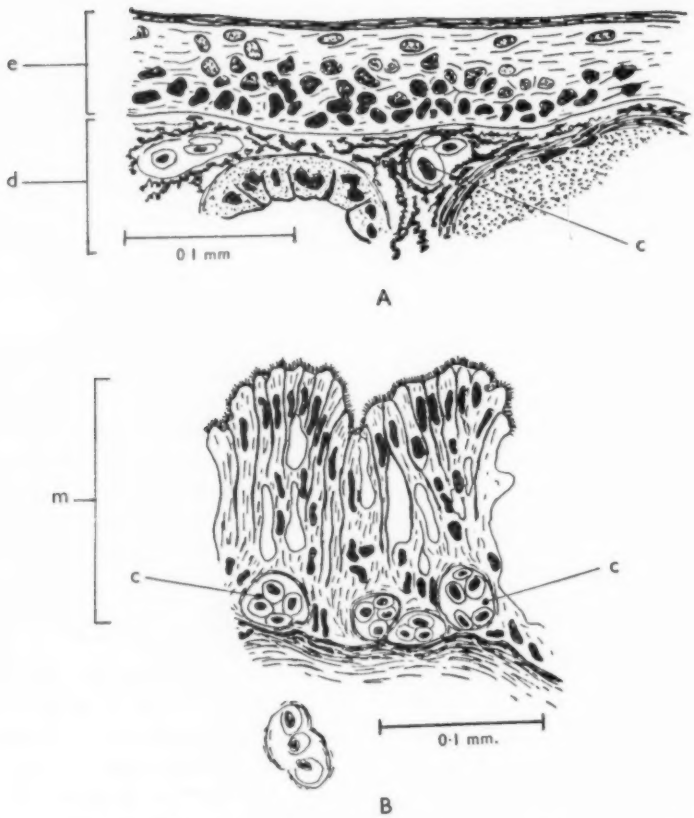


Fig. 4.—*Salamandra salamandra*. A, Epidermis. B, Oral mucosa. c, Capillaries. d, Dermis. e, Epidermis.

EUPROCTUS ASPER Dugès

Site A (Labio-nasal)	Thick, stratified epithelium (10–20) with wide capillaries at the base. Capillary loops extend into the epithelium occasionally but not very deeply.
Site B (Sphenoidal)	Epithelium gradually becoming cuboidal and thinning out to 3–6. Dermal mucous glands and a few goblet cells are present.
Site C (Spheno-oesophageal)	Solid columnar epithelium, ciliated, 3–4 cells deep. No goblet cells. Few capillaries at the base of the epithelium.
Site D (Mandibular)	Transition from the stratified epithelium of the epidermis to loose, high columnar, non-ciliated mucosa with areas of large goblet cells.

Site E (Ventro-lingual)	High columnar epithelium with some goblet cells.
Site F (Dorso-lingual)	Epithelium stratified to low columnar, 3–5 cells deep. In the centre of the area there is a large patch of goblet cells at the surface. No ciliation. Mucous glands in the substance of the tongue.
Site G (Ventro-lingual posterior)	Posterior ventro-lingual fold not well developed.
Site H (Laryngeal)	Low columnar epithelium, 2–4 cells deep with keratinized surface. Ciliation only starts at the entrance to the oesophagus.

General remarks

The oral mucous membrane of this species gives, throughout, the impression of much greater solidity than that of allied species. Apart from the naso-labial region the epithelium is not markedly well supplied with capillaries (Pl. 2, fig. 1).

EUPROCTUS MONTANUS Savi

Site A (Labio-nasal)	Sudden transition from external epidermis (8–10 cells deep) to 1–2 at upper lip. Few goblet cells. Few dermal capillaries. No ciliation.
Site B (Sphenoidal)	Cuboidal epithelium, 1–2 cells deep. No ciliation, no epithelial capillaries.
Site C (Spheno-oesophageal)	Cuboidal epithelium, 1–2 cells deep. No ciliation.
Site D (Mandibular)	Sudden transition from gular epidermis (3–5) to 1–2 at lower lip. No ciliation, no goblet cells.
Site E (Ventro-lingual, ant.)	Short anterior sublingual fold. Mucosa very thin (1–2) and much folded. Capillaries in the loosely knit dermis.
Site F (Dorso-lingual)	Mucosa 1–2 cells deep. Capillaries near the surface of the tongue. Ciliated villi without mucous glands, well supplied with capillaries.
Site G (Ventro-lingual, post.)	There is no posterior ventro-lingual fold present in this species.
Site H (Laryngeal)	Mucosa continuing very thin (1–2 cells deep). Few dermal capillaries.

General remarks

No part of the oral mucosa in this species gives the impression of respiratory function. Capillaries come nearest the surface in the dorso-lingual region where they supply the extensively developed mucous glands.

PLEURODELES WALTLI Michahelles

Site A (Naso-labial)	Mucosa cuboidal, 5–10 cells deep, non-ciliated. Capillaries in the dermis only but close to the base of the epidermis. No intraepithelial capillaries. No goblet cells.

Site B (Sphenoidal)	Epithelium cuboidal, 4–6 cells thick, ciliated. Medium sized goblet cells.
Site C (Spheno-oesophageal)	Columnar ciliated epithelium, 4–6 cells deep. Dermal capillaries at the base of the epithelium.
Site D (Mandibular)	Quick transition from external epidermis (8–11 cells deep) to oral epithelium (2–3). Dermal capillaries only.
Site E (Ventro-lingual, ant.)	Cuboidal epithelium, non-ciliated. No goblet cells. Some neuromasts. Vessels at dermo-epithelial border.
Site F (Dorso-lingual)	Deep mucous glands. Vessels in the dermis only.
Site G (Ventro-lingual, post.)	No posterior ventro-lingual fold present in this species.
Site H (Laryngeal)	Non-ciliated, low cuboidal epithelium with increasing numbers of small goblet cells. Capillary vessels at dermo-epithelial border.

General remarks

Nothing in the histological anatomy of the oral mucosa in this species indicates a high degree of gas exchange through the bucco-pharynx.

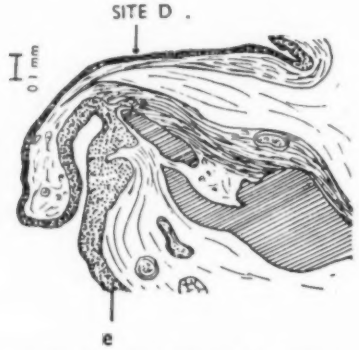


Fig. 5.—*Pleurodeles waltli*. Sagittal section through lip of mandible showing transition from epidermis to oral mucosa. The change is only one of thickness, not of structure. The epithelium is not ciliated and there are no intraepithelial capillaries. e. Epidermis.

AMBYSTOMA TIGRINUM Green. Larva.

Site A (Labio-nasal)	Gradual transition from thick epidermis (10–14 cells deep) to cuboidal oral mucosa (8–10) in the palatal region. No ciliation.
Site B (Sphenoidal)	Mucosa 8–10 cells deep, without sharp demarcation from the very cellular dermis.
Site C (Spheno-oesophageal)	Mucosa gradually thinning to 1–2. Large and small goblet cells. No ciliation. No epithelial capillaries. Blood vessels in the dermis only.

Site D (Mandibular)	Gradual transition from epidermis (8–15) to non-ciliated oral mucosa. No goblet cells. No epithelial capillaries. Mucosa 5–7 cells deep.
Site E (Ventro-lingual, ant.)	No sharp boundary of lingual region. Goblet cells gradually becoming more numerous. No epithelial capillaries.
Site F (Dorso-lingual)	Mucosa continuing without much change (4–14) Goblet cells slightly larger than in previous sites.
Site G (Ventro-lingual, post.)	Posterior lingual fold absent.
Site H (Laryngeal)	Mucosa continuing as before. No ciliation. No epithelial capillaries.

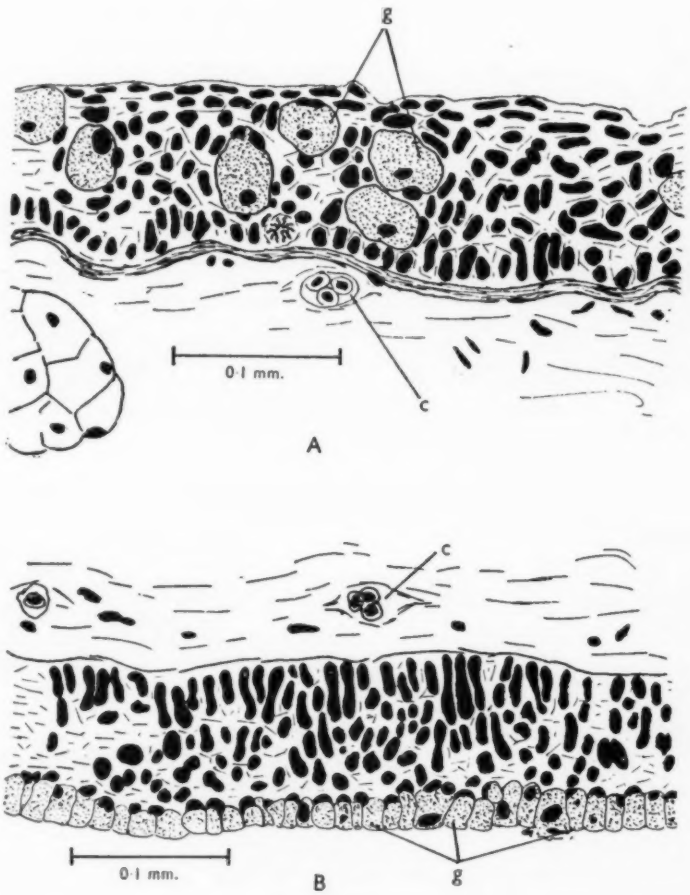


Fig. 6.—*Ambystoma tigrinum*. A. Epidermis. B. Site B. c. Capillaries. g. Goblet cells.

General remarks

The difference between the epidermis and the oral mucosa in this species is so slight as to make it appear unlikely that their function should differ much. Capillaries are sparse and confined to the dermis.

AMPHIUMA MEANS Gardiner

The oral mucous lining is uniform in all regions, the epithelium being of the low columnar, almost stratified type with a keratinising superficial cuticula and few mucus producing cells. Ciliation is absent throughout and so are intraepithelial capillaries.

The dermis is of considerable thickness and contains large blood-filled sinuses. These are largest in the mid-palatal region and ramify in the alveolar process among the teeth and the anlagen of the spare teeth. Their physiological effect is not obvious since a venous plexus of such extent must slow down the circulation rather than intensify it. There are no fine ramifications to reach the surface so as to suggest the function of gas exchange and while the building-up of new teeth may require intensive nutrition this could not explain the

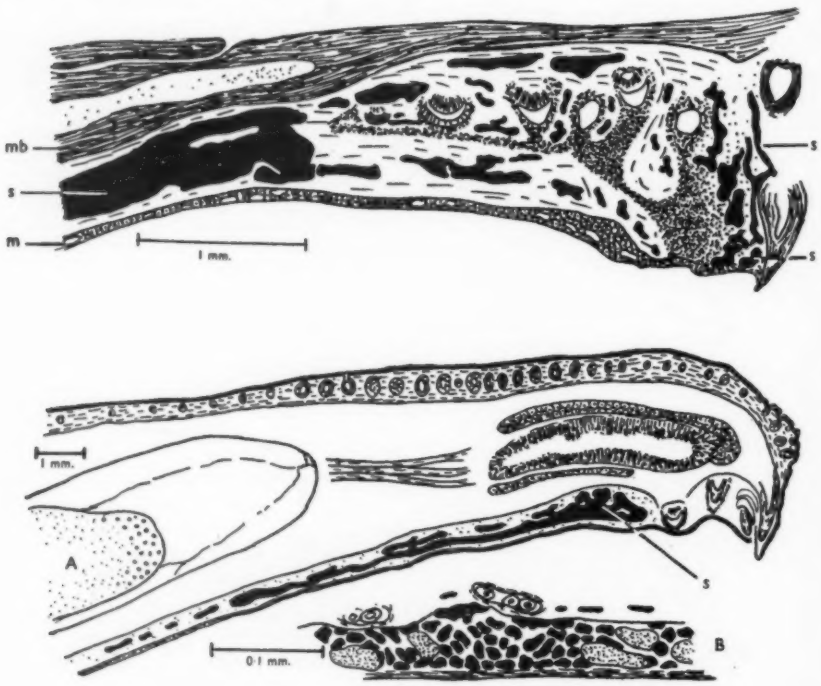


Fig. 7.—*Amphiuma means*. Top. Sagittal section through maxillary alveolar process, showing extent of dermal venous sinuses. Lower. A. Head, sagittal, paramedian, showing palatal dermal venous sinuses. B. Oral mucosa, Site A. m. Mucosa ; mb. Maxillary bone ; s. Blood sinus.

existence of such a large plexus which is obviously venous. Similar blood reservoirs can be seen in coecilians (Fig. 7). Their function there as here remains to be determined.

BATRACHOSEPS ATTENUATUS Eschscholtz

Site A (Labio-nasal)	Rapid transition from epidermis (2–4 stratified) to oral mucosa (3–5) columnar, with some medium-sized goblet cells. Capillaries at the base of the epithelium, some loops penetrating the epithelial layer. Surface ciliated.
Site B (Sphenoidal)	Low cuboidal epithelium in choanal region. No epithelial capillaries. Depth of mucosa increasing to 3–5 between sphenoidal teeth. Capillaries numerous at base of epithelium, often only 1–3 cells from the surface. Surface ciliated.
Site C (Spheno-oesophageal)	Epithelium very low (1–2) cuboidal. No ciliation no epithelial capillaries.
Site D (Mandibular)	Sudden transition from epidermis (2–3) to high columnar ciliated mucosa. Some capillaries at the base of the epithelium. Some medium sized goblet cells.
Site E (Ventro-lingual, ant.)	Thin, stratified epithelium, one cell deep. No ciliation. No surface capillaries. Tongue stalk encased in a deep sheath.
Site F (Dorso-lingual)	High columnar epithelium with deep mucous glands embedded in the substance of the tongue.
Site G (Ventro-lingual posterior)	Thin, stratified epithelium, one cell deep. No ciliation. No surface capillaries.
Site H (Laryngeal)	Columnar epithelium, 3–5 cells deep, ciliated. Small goblet cells.
Epidermis	2–3 cells deep, stratified. Dermal capillaries.

General remarks

Only in the sphenoidal region can capillaries be found separated from the surface by only a few cells. These could assist in gas exchange but they do not occur on other areas. (Fig. 8).

ENSATINA ESCHSCHOLTZI Gray

Site A (Labio-nasal)	The stratified epithelium of the epidermis changes at the alveolar process to a high columnar ciliated mucosa 10–15 cells deep. Some goblet cells are present. Capillaries are seen at the base of the epithelium. This is soon reduced to a depth of 3–5.
Site B (Sphenoidal)	Ciliated epithelium 3–5 cells deep, cuboidal. Capillaries lie at the base of the thin mucosa. They are few in number. Surface ciliated. Few goblet cells.

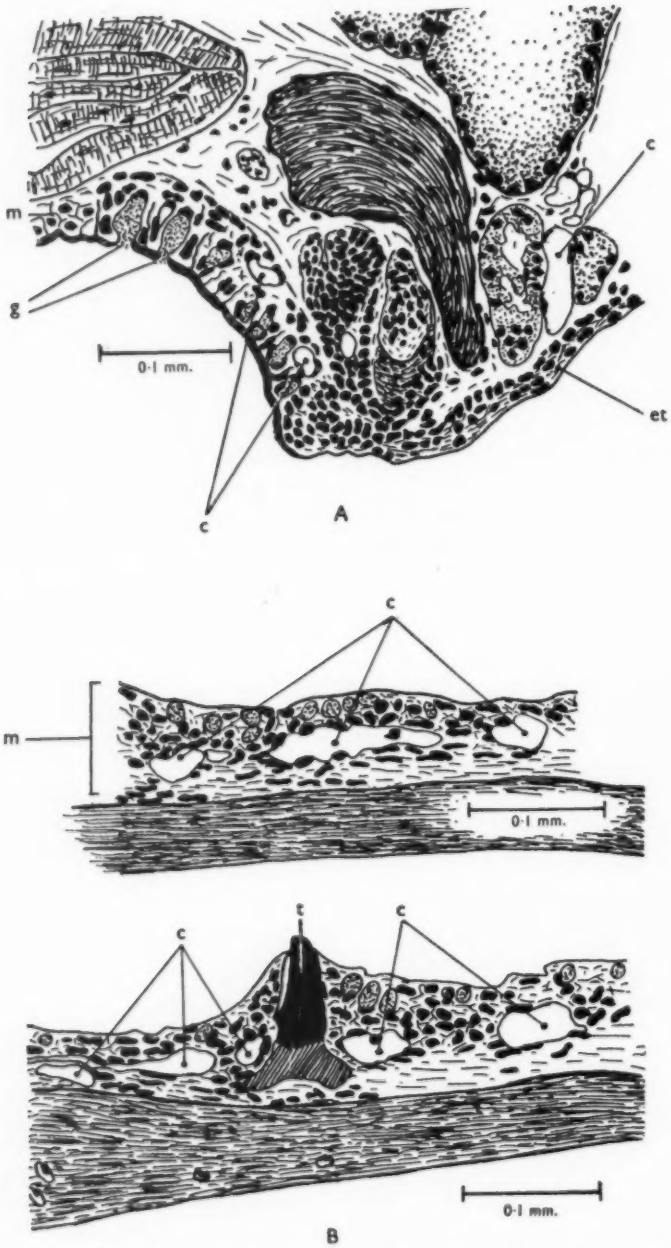


Fig. 8.—*Batrachoseps attenuatus*. A. Superior alveolar process sgt. B. Site B. c. Capillaries. et. Epithelium. g. Goblet cells. m. Mucosa. t. Tooth.

Site C (Spheno-oesophageal)	Ciliated epithelium (3–5) high columnar. Some goblet cells. Capillaries at the base of the epithelium.
Site D (Mandibular)	Transition from stratified gular epidermis at the alveolar process to a high columnar, very folded mucosa. This is at first ciliated. The ciliation is gradually reduced. A few intraepithelial capillaries can be seen. Sublingually the epithelium is reduced to 1–2.
Site E (Ventro-lingual ant.)	Stratified epithelium (1–2) increasing to cuboidal type (3–4) at anterior rim of tongue. No epithelial capillaries.
Site F (Dorso-lingual)	Deep mucous glands. No epithelial capillaries.
Site G (Ventro-lingual, post.)	Tongue stalk accommodated in a deep sheath lined with thin (1–2) stratified epithelium.
Site H (Laryngeal)	Epithelium gradually increasing to 3–5–8. There are neither goblet cells not epithelial capillaries.
Epidermis	3–5 cells deep, stratified. There is a regular capillary network between the dermal glands.

General remarks

Only a few intraepithelial capillaries were seen in site D. Their development is not extensive.

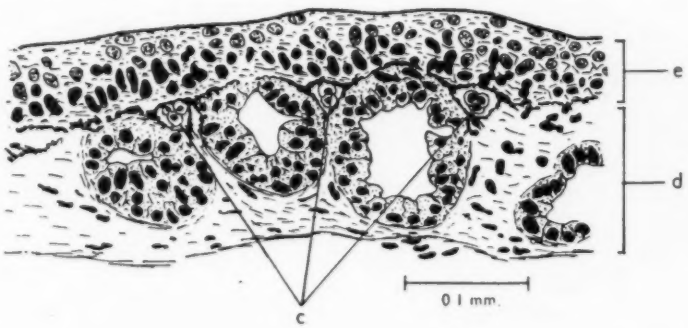


Fig. 9.—*Ensatina eschscholtzii* Skin. c. Capillaries. d. Dermis. e. Epidermis.

PLETHODON GLUTINOSUS Green

Site A (Labio-nasal)	Compact cuboid epithelium, 2–3 cells deep in vomerine region. Surface ciliated.
Site B (Sphenoidal)	Epithelium unchanged from site A, but ciliation gradually reduced. A few capillaries are found at the base of the mucosa.
Site C (Spheno-oesophageal)	Epithelium squamo-cuboidal, 3–5 cells deep, without ciliation. No epithelial capillaries.

Site D (Mandibular)	Gradual transition from gular epidermis (3–4) to high cuboidal folds at inner mandibular rim. The folds face the antero-ventral aspect of the tongue. Surface ciliated. No epithelial capillaries.
Site E (Ventro-lingual, ant.)	Sudden transition to cuboidael epithelium (2–3). No ciliation, no goblet cells, no epithelial capillaries.
Site F (Dorso-lingual)	Mucous glands abundant and penetrating deeply into the substance of the tongue.
Site G (Ventro-lingual, post.)	Cuboidal epithelium 1–2 cells deep. No ciliation. No intraepithelial capillaries.
Site H (Laryngeal)	Flat, squamous epithelium, 1–2 cells deep, gradually increasing to 2–4. Medium-sized goblet cells.

General remarks

No intraepithelial capillaries were seen in any region.

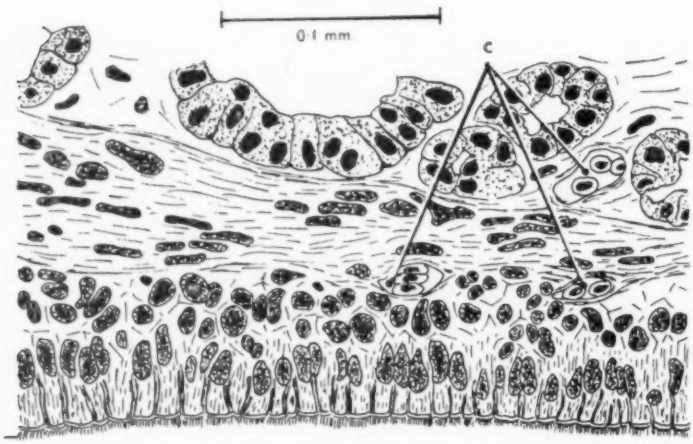


Fig. 10.—*Plethodon glutinosus*. Site B. c. Capillaries.

PSEUDOTRITON RUBER RUBER Tschudi

Site A (Labio-nasal)	Depth of epithelium 6–8 cells. One large fold of palatine mucosa. Intraepithelial capillaries present. Ciliation present. Large goblet cells lining the surface.
Site B (Sphenoidal)	Cuboid epithelium 6–8 cells deep. No goblet cells. There is a dense network of intraepithelial capillaries.
Site C (Spheno-oesophageal)	Cuboid epithelium 4–6 cells deep. Many large goblet cells present. Intraepithelial capillaries strongly developed but they do not quite reach the surface.

Site D (Mandibular)	Depth of epithelium 6–8 cells. Many large goblet cells present. Ciliation present. There is one large fold of mandibular mucosa. Intraepithelial capillaries well developed. The surface of the mucosal fold is not ciliated.
Site E (Ventro-lingual, ant.)	Flattened stratified epithelium 1–2 cells deep. No ciliation. No epithelial capillaries.
Site F (Ventro-lingual, ant.)	Mucous glands penetrating deeply into the muscular layer. No epithelial capillaries. Depth of epithelium 4–6 cells.
Site G (Ventro-lingual, post.)	Slightly folded epithelium, much flattened, 1–2 cells deep. No ciliation. No epithelial capillaries.

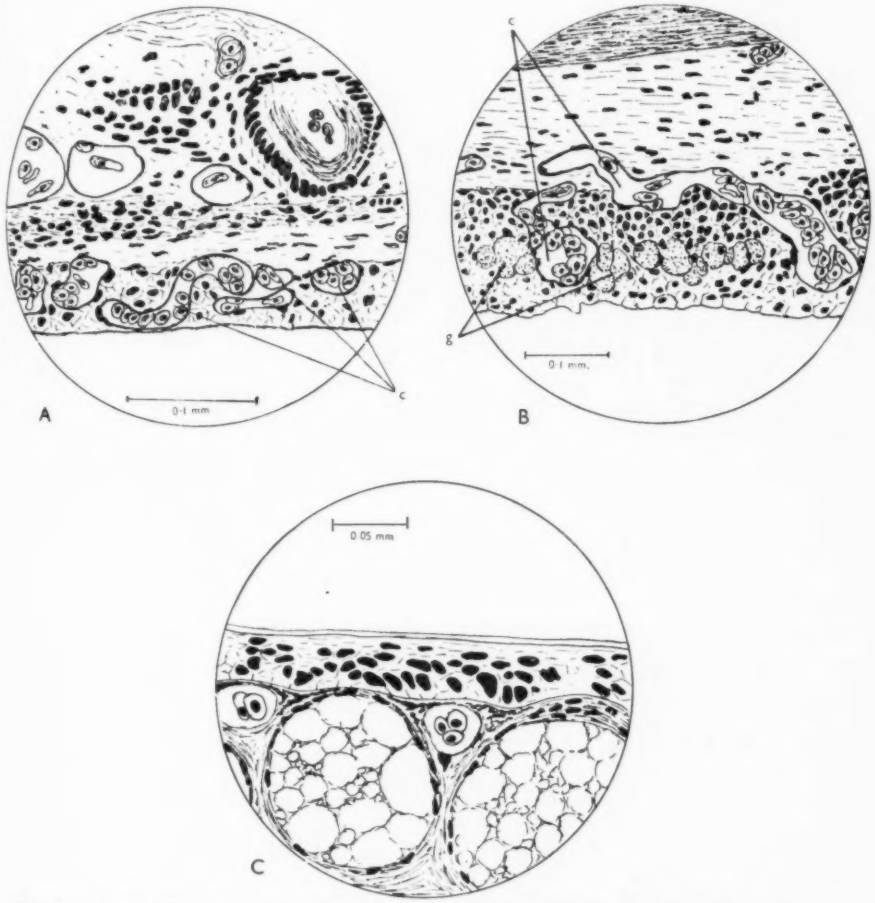


Fig. 11.—*Pseudotriton ruber ruber*. A. Oral mucosa. Region B/C. B. Oral mucosa, Region C. C. Epidermis. c, Capillaries. g, Goblet cells.

Site H (Laryngeal)	Depth of epithelium 2–4 cells with large goblet cells and well developed intraepithelial capillaries. Ciliation in the area behind the posterior margin of the tongue.

General remarks

Pseudotriton ruber presents a great exception to the rule. An extensive network of intraepithelial oral capillaries is found in sites A, B, C and D. These capillaries often penetrate the epithelium to such an extent that only their thin wall separates them from the surface (Fig. 11 A–C and Pl. 2, fig. 2). The particular specimen sectioned also refutes the assumption that an extensive surface capillary network should be incompatable with feeding. In the oral cavity of the animal appear cross sections of another, smaller amphibian which, in spite of its size does not even compress the capillaries, and although the animal swallowed must have been alive, there is no sign of injury.

DESMOGNATHUS OCHROPHAEUS Cope

Site A (Naso-labial)	Gradual transition from epidermis (2–4) to oral mucosa. A thick ridge (15–20) is found just behind the maxillary teeth. Surface not ciliated. No epithelial capillaries.
Site B (Sphenoidal)	Epithelium reduced to 1–3, ciliated, with some medium sized goblet cells. No dermis. Capillaries between mucosa and bone.
Site C (Spheno-oesophageal)	Mucosa 3–5 cells thick. No dermis. Epithelium gradually increasing to 6–8. Very few capillaries at the base of the mucosa.
Site D (Mandibular)	Rapid increase behind the mandibular teeth to a depth of 6–8 in form of a ridge with some intra-epithelial capillaries. Surface ciliated.
Site E (Ventro-lingual, ant.)	The anterior sublingual fold is short, the epithelium 1–3 cells deep with a few intraepithelial capillaries. Surface not ciliated.
Site F (Dorso-lingual)	The tongue is large and covers almost the whole floor of the mouth. It consists mainly of mucous glands which penetrate deeply into the substance of the tongue. Surface not ciliated.
Site G (Ventro-lingual, post.)	There is a sudden transition at the posterior rim of the tongue to stratified epitheliun of 1–2 cells depth. This increases opposite the posterior rim of the tongue to cuboidal epithelium (3–6). There are some intraepithelial capillaries in this region. Surface not ciliated.
Site H (Laryngeal)	Epithelium increasing to 8–10 with some intra-epithelial capillaries, then reducing to 4–6 with some medium sized goblet cells. Surface not ciliated.

General remarks

Intraepithelial capillaries which occur in sites G and H may assist in repiration. Their development is not extensive.

PROTEUS ANGUINEUS Laurenti

Site A (Labio-nasal)	Sudden reduction from epidermis of skin (8–10 cells deep) to that of the upper lip (1–2). Few goblet cells. No ciliation. Few dermal, no epithelial capillaries.
Site B (Sphenoidal)	Epithelial cuboidal, 3–4 cells deep. No ciliation. No goblet cells. Few dermal, no epithelial capillaries.

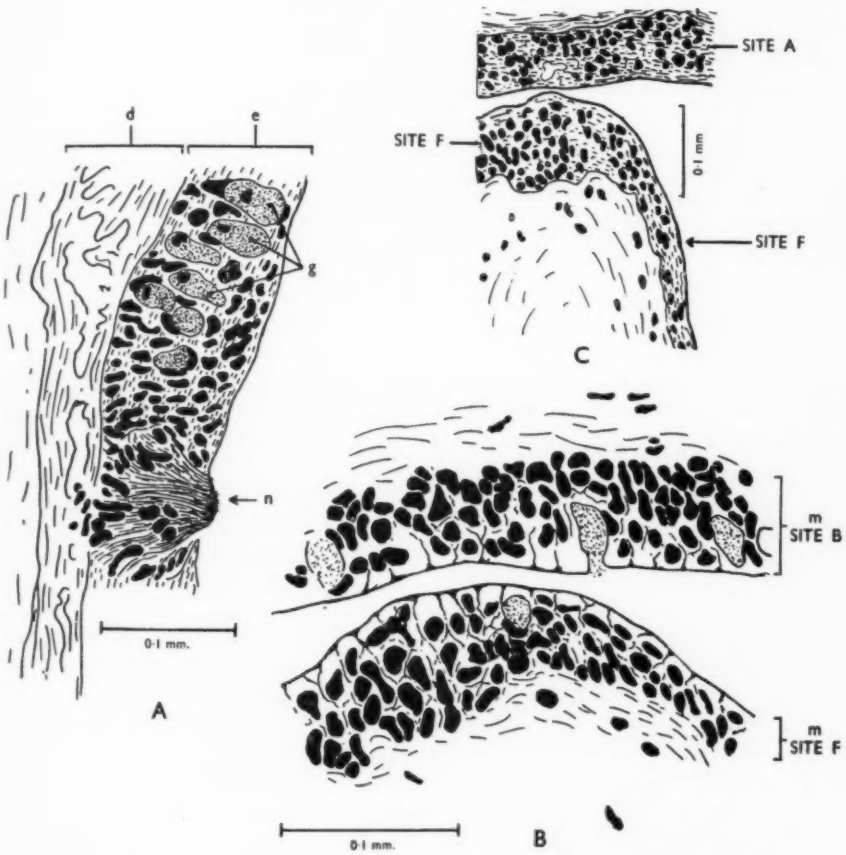


Fig. 12.—*Proteus anguineus*. A. Epidermis, dorsal region; B. Sites B and F. C. Sagittal section through tongue and palate. There is hardly any structural difference between the epidermis and the oral mucosa. There is no ciliation and intraepithelial capillaries are absent. d. Dermis. e. Epidermis. g. Goblet cells. m. Mucosa. n. Neuromast.

Site C (Spheno-oesophageal)	Epithelium cuboidal, 6–8 cells deep, non-ciliated. Few goblet cells.
Site D (Mandibular)	The external epithelium, which is 1–2 cells deep in the gular region, thickens to 8–10 at the oral rim and is 3–5 cells deep in the site D. It becomes gradually reduced to 1–2 cells at the anterior sublingual fold. No ciliation, no epithelial capillaries.
Site E (Ventro-lingual, ant.)	Cuboidal epithelial cells 1–2 deep. No goblet cells, no glands. No epithelial capillaries.
Site F (Dorso-lingual)	Gradual transition to thicker epithelium (3–4) at anterior tip of tongue. No ciliation, no glands, few goblet dells.
Site G (Ventro-lingual, post.)	There is no ventro-lingual posterior fold in this species.
Site F (Laryngeal)	Epithelium 1–3 cells deep with many small goblet cells but no ciliation and no epithelial capillaries.

General remarks

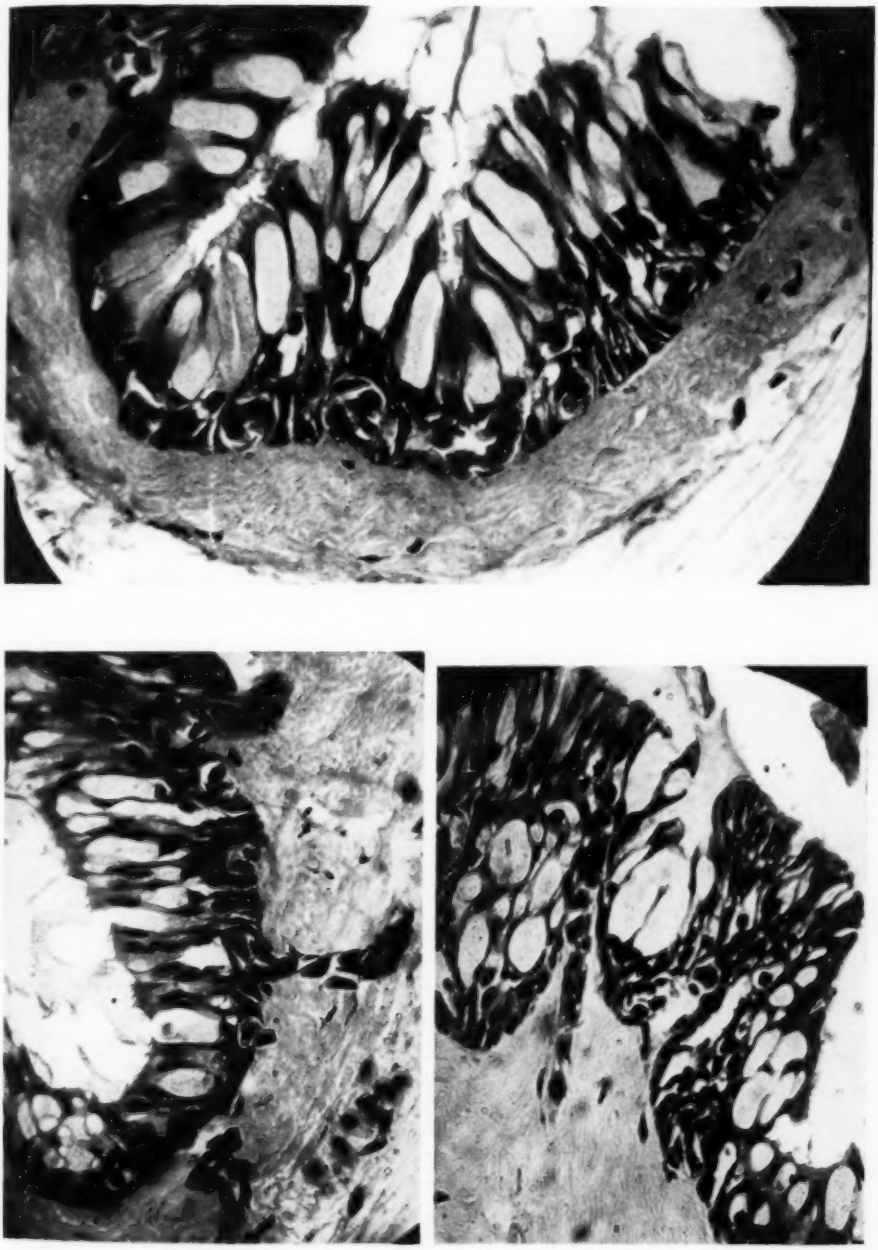
Little difference can be seen between the epidermis and the oral mucosa. Epithelial capillaries were not seen.

CONCLUSION

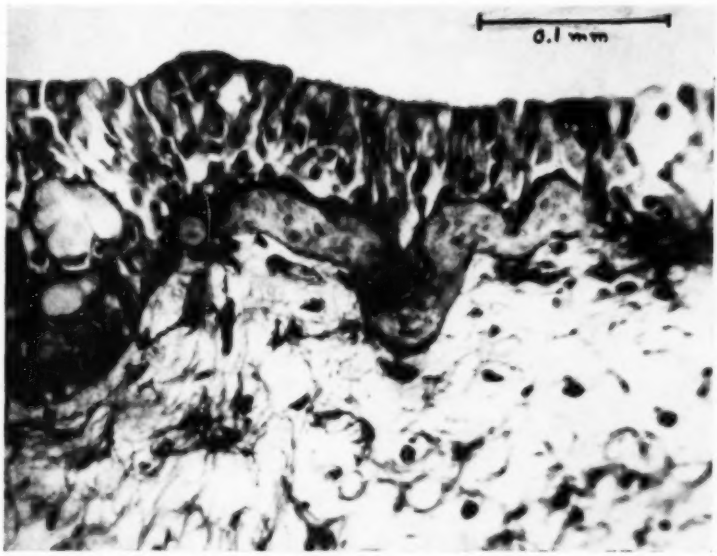
The examination of one coecilian and fourteen genera of Urodela supports on the whole the conclusion reached earlier (Elkan, 1955) ; the bucco-pharyngeal membrane of these amphibians shows—with two exceptions—no special adaptation in the direction of a respiratory membrane. The two exceptions are *Eurycea* and *Pseudotriton* the latter showing a particularly well developed intraepithelial oral capillary network. Such a network, even if it extends to the very surface, does not interfere with deglutition and could therefore have developed in all apneumonic forms. It is however absent in most of them. On the other hand if it is assumed that gas exchange in these amphibians takes place mainly by diffusion through the skin, it must be considered that the skin of all these species is not supplied with epithelial capillaries either and that the capillary network which would be instrumental in gas exchange lies only at the dermo-epidermal border. We must therefore concede that gas exchange can take place through any wet live membrane even if four to six cell layers thick and unsupplied with capillaries. If this is so, the extensive capillary network in *Pseudotriton* and *Eurycea* is difficult to explain. Further material will have to be examined to elucidate this point.

ACKNOWLEDGMENTS

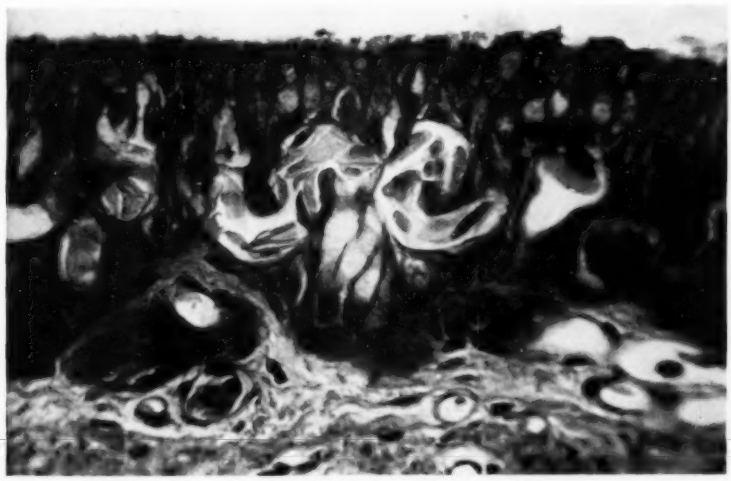
I wish to extend sincere thanks to all correspondents who have sent me live and preserved material from regions which, without their help, would have been inaccessible to me, in particular Dr N. Coiffait and Professor Vandel of the Laboratoire Souterrain, Moulis, Ariège, Mr H. Grün of Linares di Riofrio, Salamanca, Spain, Dr J. L. Hamerton of the Radiobiological Research Institute



Salamandra salamandra. Intra-epithelial capillaries in the oral mucosa.
Haematoxylin—Eosin



Euproctus asper. Region A. Oral mucosa. Capillaries at the base of the epithelium. Haematoxylin—Eosin.



Pseudotriton ruber ruber. Region A. Intra-epithelial capillaries in palatal mucosa. Methyl-Blue—Eosin—Orange G.

at the Atomic Energy Research Establishment, Harwell, U.K., Dr N. D. Richmond of the Carnegie Museum Pittsburgh, U.S.A., Dr F. J. Simmonds of the Imperial College of Tropical Agriculture, St. Augustine, Trinidad, Dr R. C. Stebbins of the Museum of Vertebrate Zoology, Berkeley, California, and Professor M. Zei of the Department of Zoology, The University, Ljubljana.

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THE GROWTH OF CONFINED COLONIES OF THE WILD HOUSE-MOUSE (*MUS MUSCULUS* L.) : THE EFFECT OF DISPERSAL ON FEMALE FECUNDITY

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(With 3 figures in the text)

CONTENTS

	Page
Introduction	357
Methods	358
Results	358
(a) Post-mortem examination of colony E	358
(b) Dispersal of colony F	358
(c) Dispersal of part of colony G	360
(d) Dispersal of colony B	361
Discussion	363
Summary	365
References	365

INTRODUCTION

In an earlier communication (Crowcroft & Rowe, 1957) it was suggested that the most important factor limiting population growth in four colonies of house mice was the low fecundity rate of the females. The vulva of a female reared under crowded conditions either failed to open, or resealed after a short period. Post-mortem examination of the females of three of the colonies (A, C and D) showed that an imperforate condition was associated with an inactive ovary, thread-like uterus, and excessive fat deposits. The reduction in fecundity was particularly striking in colony B, in which reproduction ceased. The fecundity of male mice was apparently unaffected by the crowded conditions.

Three other colonies (E, F, and G), set up under the same conditions as the other four, had to be eliminated earlier owing to pressure of work. Their initial growth followed a similar pattern. Colony E was killed after eight months, and the mice examined internally to check the validity of the adopted criteria of fecundity. Dr Charles H. Southwick kindly assisted, thus ensuring

* Formerly Infestation Control Division, Ministry of Agriculture, Fisheries and Food.

that direct comparisons could be made between our respective results (see Southwick, 1955 a and b).

Before being killed, the remaining colonies F and G were used to investigate the effect on fecundity of dispersal into larger pens. Colony B, in which no reproduction had occurred for over six months, was also allowed to disperse into a larger pen.

METHODS

Each colony was founded with one adult male and two adult females. The original pens were six feet square, with sheet-metal sides two feet high, and provided with eight wooden nest-covers (see Crowcroft & Rowe, 1957). Whole oats and wheat, " Diet 41 " (Bruce & Parkes, 1949), and water, were provided at numerous points and replenished frequently. Hay was supplied for nesting material. The animals were individually marked at an early age by toe-clipping. Fortnightly (later monthly) censuses were carried out by placing sheet-metal barriers around the nest-covers and examining their contents in turn.

The mice from pen G were released within the new pens, but those in F and B were permitted to disperse through a single small hole.

RESULTS

(*a*) *Post-mortem examination of colony E*

Female laboratory mice are known to attain sexual maturity within eight weeks from birth (Parkes, 1925 ; Engle & Rosasco, 1927). The age at which free-living wild house mice begin to reproduce is not known. Laurie (1946) found, however, that over 95 per cent of females between 10·0 g. and 12·5 g. in weight, caught in food stores, were fecund. Judging by the growth rates of wild mice in large pens, this weight range corresponds with an age of about six to eight weeks.

When colony E was eliminated after thirty-two weeks, fifty-nine animals were present and there were already signs of lowered fecundity among the females. Corpora lutea were present in only thirteen of twenty-four females more than eight weeks old (Table 1) and two of these (Nos. 15 and 19, Table 1) appeared to be reverting to a non-breeding state. None of these animals weighed less than 11·5 g. The general correlation between the external and internal criteria of fecundity was established, exceptions being visibly pregnant or lactating animals (Table 1).

(*b*) *Dispersal of colony F*

The early growth of colony F was also similar to that of the other colonies. After thirty-two weeks it was allowed to disperse into a larger pen of approximately 130 square feet, containing additional nest-covers and feeding points. Thereafter it grew at a faster rate than any other colony and its total numbers soon exceeded those of B (Fig. 1).

At dispersal only five of the fifteen females of adult age, born in the pen were perforate (33 per cent), whereas eleven (73 per cent) were perforate two weeks later. Thus the increase in gross reproductive rate after dispersal (Table 2) was apparently due to increased female fecundity. The result was

TABLE 1

Age, weight, and reproductive condition of colony E females.

No.	Age in days	Weight in g.	Reproductive condition			Remarks
			Vulva perforate	Diameter of uterus	Corpora lutea present	
1	?	21·5	+	2 mm.	+	original female
2	201	23·6	+	2 mm.	+	pregnant
3	182	17·0	−	2 mm.	+	placental scars
4	173	15·7	+	2 mm.	+	
5	172	12·0	+	2 mm.	+	copulation plug
6	148	18·9	+	2 mm.	+	pregnant
7	148	16·9	−	2 mm.	+	placental scars
8	148	17·1	−	2 mm.	+	pregnant
9	148	14·4	+	2 mm.	+	abundant fat
10	128	14·4	+	2 mm.	+	
11	127	13·7	−*	thread	−	abundant fat
12	127	22·4	+	2 mm.	+	pregnant
13	114	12·4	+	2 mm.	+	oestrous
14	114	14·4	+	2 mm.	+	oestrous
15	110	16·4	−*	1 mm.	+	abundant fat
16	103	13·8	−	thread	−	abundant fat
17	95	14·4	−	2 mm.	+	pregnant
18	95	13·1	−*	1 mm.	−	abundant fat
19	93	14·4	−	1 mm.	+	abundant fat
20	93	12·8	−	1 mm.	−	abundant fat
21	73	12·6	−	thread	−	abundant fat
22	73	12·3	−	thread	−	abundant fat
23	73	13·3	−	thread	−	abundant fat
24	72	13·2	−	1 mm.	−	abundant fat
25	69	11·5	−	thread	−	abundant fat

* Not completely sealed.

TABLE 2

Reproduction and infant survival in colony F

Period (weeks)	Number of young born	Average number of adult females present	Gross reproductive rate	Infant survival rate	Average total number of mice*
17–20	4	4·0	1·00	1·00	22
21–24	8	7·0	1·14	0·88	30
25–28	6	11·7	0·51	1·00	34
29–32	15	15·5	0·97	1·00	43
33–36	42	15·5	2·71	0·90	77
37–40	41	18·3	2·25	0·90	113
41–44	28	35·0	0·80	0·88	136
45–48	27	57·5	0·59	0·85	161

* Nearest whole number

not clear cut however, as some of the litters contributing to this increase must have been conceived before dispersal.

The rapid increase in numbers in the new pen during the eight weeks after dispersal caused a renewal of the crowded conditions. Four months after dispersal the mice were killed and post mortem examination showed that 75 per cent of the adult females were non-fecund (79 per cent imperforate).

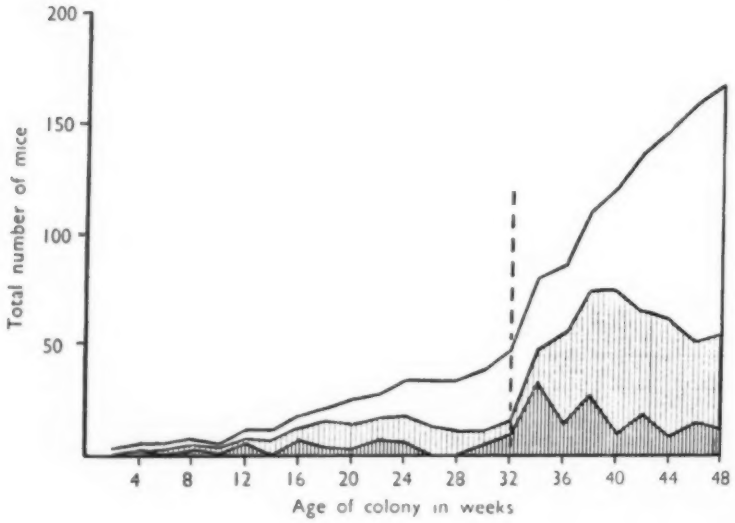

Fig. 1.—The growth of colony F. The broken vertical line marks the time of dispersal into a larger pen (bottom graph, infants ; middle graph, infants plus juveniles ; top graph, total numbers).

(c) *Dispersal of part of colony G*

The existence of a causal relationship between overcrowding and reduced female fecundity was suggested, although not proved, by the changes in colony F following dispersal. Certainly no comparable rapid increase in numbers occurred in the other pens. The effect of dispersal on the fecundity of crowded females was further investigated with colony G. As in the other colonies the high initial rate of increase was not maintained (Fig. 2 a). After forty weeks the twenty-one adult females were divided into two groups of similar size and age composition. Ten females (nine imperforate) and eleven adult males were released in a new pen of approximately 225 square feet (colony G i). The other eleven females (ten imperforate), together with the rest of the population, consisting of twenty adult males and seventeen juvenile mice, were transferred to a new pen identical with the original (colony G ii). Eight days later the females in both groups were examined. With only one exception

those in the large pen had become perforate, but no change had occurred in the reproductive condition of those in the small pen.

The increase in numbers of G i during the following three months confirmed that the females had become fecund. No similar increase took place in G ii (Table 3, Fig. 2 b). In both colonies some deaths of young occurred as a consequence of observer interference.

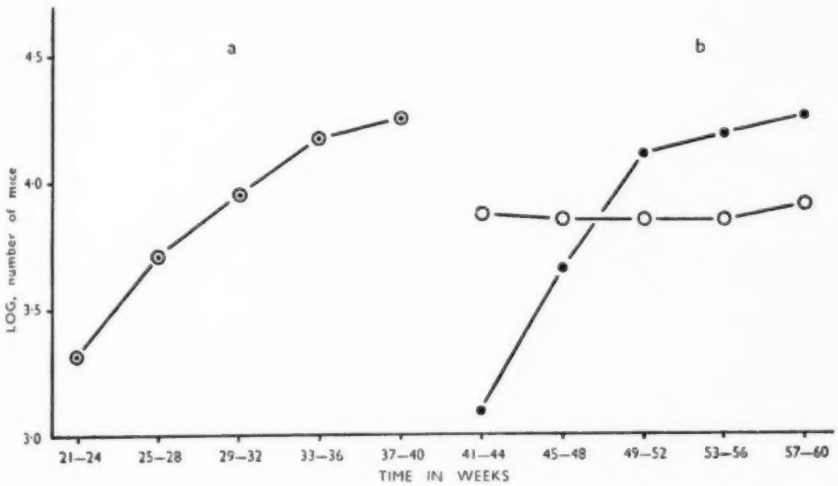

Fig. 2.—(a) The rate of growth of colony G before division into two parts.
(b) The rates of growth of the two new colonies G i (●) and G ii (o). For explanation see text.

(*d*) *Dispersal of colony B*

The growth of this colony has already been described (Crowcroft & Rowe, 1957). It grew more rapidly than any other and contained 150 animals after forty weeks. There were no further births and after the forty-eighth week the population consisted entirely of mice of adult age and weight. At the end of the seventy-fourth week the surviving 140 mice were given access to an adjacent pen of approximately 400 square feet. External examination of the females just before dispersal showed that only one of the sixty-seven was perforate. Eight days after dispersal thirty-four females were perforate; nineteen of the twenty-nine nesting in the new area (66 per cent), and fifteen of the thirty-eight (40 per cent) which had remained in the original pen. The apparent increase in female fecundity was confirmed by the rapid increase in the birth rate. As infant mortality remained low, the colony increased to 382 mice within ten weeks of dispersal. Unfortunately it was not possible to maintain it for a longer period.

TABLE 3

Reproduction and infant survival in colony G.

	Period (weeks)	17–20	21–24	25–28	29–32	33–36	37–40	41–44	45–48	49–52	53–56	57–60
G	Number of young born	13	9	16	9	14	4					
	Average number of adult females	2·0	4·3	6·8	11·0	16·5	21·3					
	Gross Reproductive Rate	6·5	2·1	2·4	0·8	0·9	0·2	—	—	—	—	—
	Infant Survival rate	0·9	1·0	0·9	1·0	1·0	0·0					
	Average total number of mice*	18	28	41	52	65	70					
Gi	Number of young born							2	26	24	16	36
	Average number of adult females							11·0	10·5	10·0	14·8	25·5
	Gross reproductive rate	—	—	—	—	—	—	0·2	2·5	2·4	1·1	1·4
	Infant survival rate							0·0	1·0	0·8	0·3	0·4
	Average total number of mice*							22	39	61	66	71
Gii	Number of young born							0	3	0	5	10
	Average number of adult females							17·0	21·5	21·0	21·0	21·0
	Gross reproductive rate	—	—	—	—	—	—	0·0	0·1	0·0	0·2	0·5
	Infant survival rate							—	0·0	—	0·0	1·0
	Average total number of mice*							48	48	47	47	50

* Nearest whole number

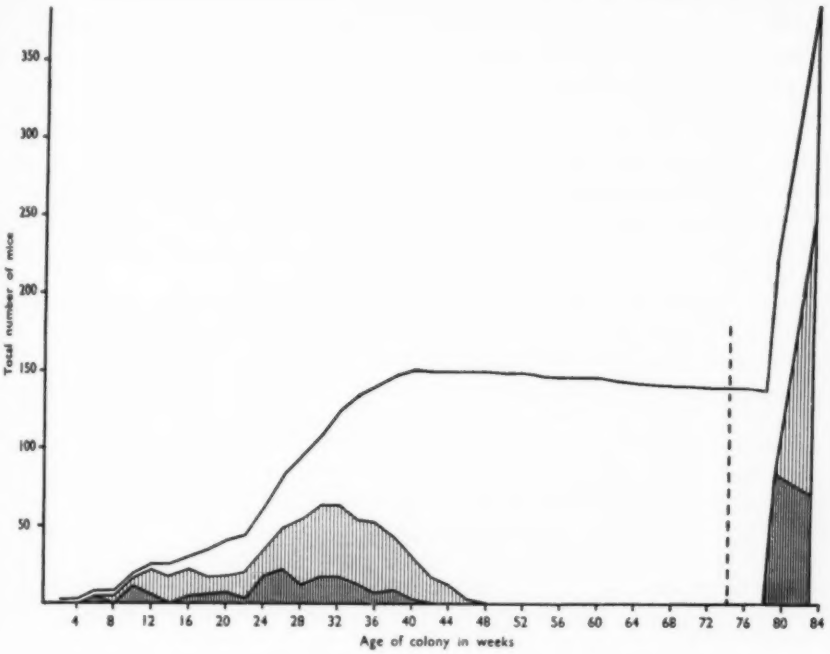

Fig. 3.—The growth of colony B. For explanation see Fig. 1.

DISCUSSION

Failure of the females to attain or to maintain a normally fecund condition was the principal cause of population limitation in these colonies. The increase in fecundity following dispersal is taken as evidence that some consequence of confinement or overcrowding was responsible for the low fecundity. Subnormal reproduction in confined colonies of rodents has been ascribed to physiological disorders caused by fighting (Clarke, 1955 ; Christian, 1956). The female mice were seldom involved in fights, however, and none was ever found with bites or scars. They spent most of their time crowded together within the nest-covers, from which they made excursions for feeding or exploration. Occasional local disturbances due to the fighting of certain males may have constituted an indirect form of " stress ". Non-fecund females with thread-like uteri and excessive fat deposits were also prominent in the colony studied by Strecker & Emlen (1953), and these were able to congregate within large shelters in a similar way. In that colony, as in those we studied, the anoestrous condition may have been associated with lack of exercise rather than with an applied stress. Schneider (1946) produced a striking increase in the fecundity of caged wild house mice by introducing exercise wheels. Dispersal and establishment in territories, with greater freedom of movement than formerly, may have had a similar effect.

Christian (1956) described the effects of stress on reproductive performance in confined colonies of wild house mice. There was a significant increase in intra-uterine mortality as compared with isolated pairs, and failure in lactation was suspected. In addition, a delay in onset of puberty might have occurred in the females, but as they were not individually marked this could not be investigated. The factor actually limiting population size at the conclusion of those experiments appeared to be mortality of the young (Christian, 1956, Figs. 1–5), for the statement that birth rates also underwent a " steady decline " with increasing population density until they " approached zero " does not appear to be adequately supported by the data presented (Christian, 1956, Fig. 5).

The high survival rate among both infants and juveniles, reported in our earlier communication (Crowcroft & Rowe, 1957) is in contrast with the high mortality in these age groups found by other workers (Brown, 1953, Southwick 1955 a and b, Christian, 1956), but the survival of young born in confinement is undoubtedly greatly influenced by the nature of the physical environment in which the mice are forced to live. This is usually designed to fulfill the needs of the investigator rather than those of the experimental animals. It cannot be stated with certainty which, if any, of the experimental conditions that have been imposed on wild house mice provide an environment in which the normal behaviour and social relationships of the animals can be exhibited. It is reasonably certain, however, from our observations on wild mice kept under diverse conditions, that the deaths of unweaned mice are more likely to be caused by intraspecific strife when the nest boxes are small, with a single opening, than when they are large, with a " through passage ". Further, deaths after weaning are inevitable in large cages provided with insufficient cover to permit frequent respite from persecution.

If such " mechanisms of population control " are so dependent upon specific experimental conditions, we must continue to question their importance in free-living populations. Lowered fecundity in response to high numbers has not been found in any naturally occurring house-mouse population. Even in British corn ricks, which supply the most favourable habitat for rapid increase, population densities approaching those in our colonies have not been observed. Thus this particular self-regulatory mechanism may operate at densities which are seldom, if ever, attained by free-living populations because of losses from other causes.

SUMMARY

1. Post-mortem examination of female house mice from a confined population showed a higher proportion of non-fecund females than would be found in a wild-caught sample of similar age composition.

2. A similar population was allowed to disperse into a larger pen, whereupon the reproductive rate increased. The result was not clear-cut, however, as the increase began too soon to be attributable to dispersal alone.

3. Another similar population was divided into two colonies of unequal size. Non-fecund females transferred to a new large pen with few other mice

became fecund and reproduced successfully, while those placed in a new small crowded pen remained non-fecund.

4. A completely adult population in which no litters had been born for over six months was allowed to disperse into a large pen. A majority of females became fecund and conceived within about one week. The numbers were doubled within eight weeks.

5. The results suggest the existence of a self-regulatory mechanism, which operates at population densities seldom, if ever, reached in free-living populations.

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THE YOLK-SAC OF THE MOLE *TALPA EUROPAEA*

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(With 3 plates)

CONTENTS

	Page
Introduction	367
Material and methods	367
Results	369
The relations of the foetal tissues and the uterine wall	369
The endometrium	371
The vascular yolk-sac placenta	371
The avascular yolk-sac placenta	373
Reichert's membrane	376
The yolk-sac splanchnopleur	376
The yolk-sac fluid	377
Discussion	379
Summary	384
Acknowledgment	385
References	385
Explanation of the plates	386

INTRODUCTION

In previous studies the structure and development of the yolk-sac placentae in *Erinaceus europaea* and *Putorius furo* have been described, together with some observations on the yolk-sac contents in these species (Morris, 1953). In *Erinaceus* implantation is of the interstitial type and although the yolk-sac persists to term it is of little importance as a placental structure in late pregnancy (Morris, 1957). The placentation of *Talpa europaea* has been described by Strahl (1892) ; implantation is of the central type and the yolk-sac persists to term. An investigation of the endometrium, yolk-sac placentae and decidua of *Talpa* involving the use of several histological and histochemical methods is reported here, together with certain data concerning the fluid contents of the yolk-sac, for comparison with the conditions which have been described in other forms.

MATERIAL AND METHODS

Material was collected in Caernarvonshire in 1949 and 1950, and in Nottinghamshire in 1955 and 1956. In North Wales females in oestrus were trapped in late March and the first visible pregnancies were obtained during the first week of April. Pregnant females were obtained throughout April, May and early June. In Nottinghamshire the season begins earlier ; some early

pregnancies were obtained in the second week of March. Pregnant females were trapped throughout March and April, and in May most of the females obtained were either parous or in very late stages of pregnancy.

A total of 132 females was obtained, of which eighty-two contained gravid uteri and twenty-one were non pregnant females in oestrus. Sixteen of the gravid uteri contained embryos in varying stages of reabsorption.

At autopsy the uteri of the oestrous females were removed and small pieces were fixed in various fluids. The implantation swellings of the pregnant uteri were separated and similarly treated. The conceptuses from animals in very late stages of pregnancy were sometimes slit open laterally and the embryos removed, whereupon the uterine wall, placentae and attached foetal membranes were fixed in one block. As far as possible only material obtained from animals which were caught alive or were fresh dead (i.e. trapped within a two hour period before autopsy) was used for the histochemical procedures.

A series of swellings was fixed in aqueous Bouin's fluid and preserved in 70 per cent alcohol. These were later serially sectioned at 10 μ and stained in Ehrlich's haematoxylin and 1 per cent aqueous eosin. Some Zenker fixed material was stained by the Azan method of Heidenhain.

The following techniques were applied to sections of three of the non-pregnant uteri of oestrous females and to a series of seven conceptuses ranging from early stages of pregnancy in which the blastocysts were free in the uterine lumen to very late stages (crown-rump length 29 mm.).

PAS reagents and Best's carmine method were used on material fixed in Rossman's fluid. These techniques were performed on sections with and without preliminary exposure to saliva at 37° C for one hour, to differentiate between glycogen and other carbohydrates.

The methyl-green pyronin method for RNA was employed on material fixed in Zenker's fluid. RNA was extracted from control sections by immersion in 10 per cent perchloric acid at 4° C for sixteen hours.

Material fixed in cold acetone or formalin and formalin fixed frozen sections were used to show alkaline phosphatase (Gomori, 1941). Turnbull blue reagents and Perl's method for ferric iron were applied to material fixed in 10 per cent neutral formalin.

Frozen sections were cut from gelatine embedded material which had been fixed in either 10 per cent formalin or 10 per cent formal-calcium. Selected sections were stained with Sudan black and the acid haematin method and the pyridine extraction test (Baker, 1946) were used on some material.

The following techniques and stains were applied to material which had been fixed in either Zenker's fixative, Bouin's fluid or 10 per cent formalin: Weigert's resorcin fuchsin for elastic tissue, Gomori's silver method for the impregnation of reticulum (1937), Lillie's allochrome method for connective tissues (1951), Masson's trichrome stain, orange G and Van Gieson's stain.

Some material was fixed in Champy's fluid or Flemmings without acetic acid, after fixation some was post-osmificated at 37° C for periods varying from twenty-four to seventy-two hours. A few swellings were fixed in Helly's fluid, postchromed, sectioned and stained by Kull's triple stain.

Stained and unstained sections of material which had been variously fixed, and also frozen sections of formalin fixed material were examined in polarized light.

A considerable part of the material obtained was used to determine the concentration of protein nitrogen in the yolk-sac fluid. Conceptuses were removed and rapidly frozen in a tube containing isopentane cooled in a Thermos flask containing a mixture of 70 per cent alcohol and solid carbon dioxide. The yolk-sac fluid was later dissected out as a globule of ice which was then thawed (Brambell & Hemmings, 1949). The fluid was centrifuged and transferred to a tube for weighing. The amount of yolk-sac fluid obtained from very early and very late stages of pregnancy was small and in such cases the fluid from a number of swellings in the same uterus was pooled.

A small quantity of human thrombin solution was added to some of the yolk-sac fluid samples to determine the presence or absence of fibrinogen. The remainder was used to determine the concentration of protein nitrogen by the simplified ultramicro Kjeldahl technique described by Shaw & Beadle (1949). Serum samples were taken from those animals caught alive, and the protein nitrogen concentration of the serum was determined by micro Kjeldahl, for comparison with that of the yolk-sac fluid.

RESULTS

The relations of the foetal tissues and the uterine wall

The placentation of *Talpa europaea* has been described by Strahl (1892), and by Vernhout (1895). Implantation is of the central type, the embryonic plate being antimesometrial in position. The blastocysts grow to a comparatively large size free in the uterine lumen and they first became attached to the uterine tissues along the lateral walls—as seen in transverse section—of the antimesometrial region of the endometrium. Here the trophoblast has thickened and in this region the vascular yolk-sac placenta will be first formed. In early stages of pregnancy the glandular zone of the antimisometrial region —extending over about two-thirds of the circumference of the uterus—is very much thicker than that of the mesometrial region.

The extension of the area vasculosa is rapid, and by the time amniogenesis is finished it has almost completed its extension between the trophoblast and the endoderm along the walls of the thickened antimesometrial mucosa. At this stage the mesometrial wall of the blastocyst is not attached to the uterine tissues. The vascular omphaloidean placenta attains its greatest extent a little later in development, when the vascular allantois has been formed and has extended across the exocoel but has not yet fused to the chorion. Subsequently the relative area of the vascular omphaloidean placenta decreases, and by the 5 mm. stage only a very small area exists in which the vitelline circulation is adjacent to thickened uterine mucosa. At the 9 mm. stage the exocoel has extended to completely separate the vascular yolk-sac splanchnopleur from the chorion, and vascular omphaliodean placentation has been terminated. Shortly after the completion of amniogenesis the avascular mesometrial wall of the blastocyst becomes attached to the uterine epithelium

of the narrow mesometrial region of the mucosa at a number of scattered points. Later, at the 3·5 mm. stage this attachment has become far more extensive so that the trophoblast adheres to the mesometrial uterine epithelium over a wide area—except in a circular zone around the blastocyst. In this zone, which is situated well below the equator of the conceptus, the trophoblast is bathed by the contents of the uterine lumen and this unattached zone of trophoblast is maintained throughout pregnancy, although its relative extent is very considerably reduced in late stages.

Following the attachment of the trophoblast to the uterine epithelium of the thickened antimesometrial mucosa the epithelial cells lose their boundaries and form a symplasma (Strahl, 1892). This symplasma persists and forms the syncytical covering of the trophoblastic villi which are formed in this region. These villi, when first formed, are solid finger-like structures projecting into the mucosa, and they generally remain in this condition throughout the duration of vacular omphaloidean placentation. Occasionally some of the more antimesometrially situated villi become partly hollowed out and filled with avascular mesoderm. The decidual tissue becomes more vascular and in transverse sections maternal capillaries can be seen immediately underlying the trophoblast. At its greatest development the vascular omphaloidean placenta is endotheliochorial in character ; the maternal and foetal blood circulations are separated by the maternal endothelium, the trophoblast, the mesenchyme and the foetal endothelium of the vitelline vessels.

Strahl (1892) describes and illustrates the trophoblast of the blastocyst adhering to the uterine epithelium of the mesometrial mucosa in early and late stages of pregnancy. Vernhout (1895), considers that the uterine epithelium of the mesometrial mucosa is disrupted and eventually destroyed by the trophoblast cells and that the trophoblast tissue forms an irregular layer on the surface of the mesometrial mucosa. Prior to the initial attachment of the trophoblast in this region of the uterine wall the uterine epithelium forms a regular layer of columnar cells about 20 μ in height. Once attachment is effected the uterine epithelium undergoes retrogressive changes ; the continuity of the epithelium is disrupted and in many places it becomes detached from the underlying connective tissue of the mucosa. By the 10 mm. stage this process is advanced and the uterine epithelium over a considerable extent of the mesometrial mucosa has disappeared. Trophoblastic elements can frequently be seen extending below the degenerating uterine epithelium, which is either lifted away from the mucosa or becomes rolled up into a mass of degenerating tissue. The uterine glands in this region are flask-like structures which open by means of very short ducts. In certain regions the trophoblast can be seen extending down the necks of these uterine glands thus freeing the degenerating glandular epithelium from the sub-epithelial connective tissue (Pl. 2, fig. G).

It has been noted that in a circular zone situated below the equator of the conceptus the trophoblast is not attached to the uterine tissues. In this zone, during the early stages of pregnancy, the uterine epithelium appears intact and normal, but in late stages when the relative extent of this zone is greatly reduced, the epithelium occasionally appears degenerate (Pl. 2, fig. I) and in

some areas has been sloughed off. The trophoblast of the yolk-sac wall in this free zone is formed of a fairly regular layer of columnar cells which in later stages attain a height of 25 μ to 30 μ. The trophoblast of the mesometrial attached region is far less regular and generally is in the form of a double layer (Pl. 2, fig. H). The upper layer, which forms an integral part of the avascular yolk-sac wall, is connected at numerous points to a lower layer which is intimately attached to the connective tissue of the mucosa. The uterine glands of the mesometrial mucosa, which is now highly vascular, open by means of short ducts into the spaces within the complex trophoblast layer. The condition of this avascular yolk-sac placenta in different stages of pregnancy will be described later.

The endometrium

The cytoplasm of the uterine and glandular epithelia of the oestrous uterus is rich in RNA, and a strong staining reaction is obtained particularly in the distal cytoplasm of the cells of these tissues after the application of methyl-green pyronin reagents. The reaction is equally intense in the deeper coiled portions of the uterine glands as in the surface uterine epithelium. The cytoplasm of the subepithelial connective tissue contains very little RNA.

Finely particulate material which stains intensely with PAS reagents is present in the distal cytoplasm of the cells of the uterine and glandular epithelia and also in the lumina of the uterine glands. A similarly intense staining reaction is obtained in these sites after saliva treatment. Best's carmine method reveals that no discernible glycogen is present either in the epithelial layers or in the subepithelial connective tissue of the uterus.

Lipoidal inclusions, stainable with Sudan black and osmic acid, are present in the cytoplasm of the epithelial tissues of the oestrous uterus. This material is mainly concentrated in the distal cytoplasm of the cells and is generally finely particulate. There is no noticeable difference in the amount of this material present in the surface uterine epethelium and in the glandular epithelium. Kull's method for mitochondria reveal the strongly fuchsinophil particulate material present in these tissues, the major concentration occurring at the distal ends of the epithelial cells.

In the oestrous uterus of *Talpa* alkaline phosphatase is present in the columnar cells of the uterine and glandular epithelia. An equally intense reaction is obtained in these two tissues and some reaction is also obtained in the lumina of the uterine glands (Pl. 1, fig. A).

No positive reactions for iron were obtained in the endometrium of the oestrous uterus after the application of Turnbull blue reagents and Perl's method for ferric iron.

The vascular yolk-sac placenta

A vascular yolk-sac placenta is soon established over the thickened antimesometrial mucosa. The area vasculosa spreads rapidly and by the time amniogenesis is completed the vascular omphaloidean placenta is of considerable extent. From this stage of pregnancy onwards its relative extent diminishes and by the 9 mm. stage the exocoel has separated the vascular yolk-sac splanchnopleur from the chorion.

Throughout the early phase of gestation the trophoblastic villi which are formed, and which penetrate deeply into the decidual tissue of the antimesometrial uterine wall, generally remain as solid finger-like structures. Subsequently they become hollowed out, a process which may commence during the period of vascular omphaloidean placentation, and later they become filled with mesenchyme. Maternal blood vessels—with intact endothelia—frequently lie immediately adjacent to the trophoblast of these villi.

Strahl has described the persistance of certain of the glands in this region of the uterus and the ensuing formation of the dome-like structures of columnar trophoblast cells over the glandular openings. These structures are essentially similar to the *areolae* which have been described in the sheep and horse (Amoroso, 1952), and they are first formed during the period of vascular omphaloidean placentation (Pl. 2, fig. F). They persist into late stages of pregnancy. The cavities of the aerolae are filled with glandular secretions which are presumably absorbed by the columnar trophoblast cells of the domes and transmitted to the vitelline circulation. At these sites some extravasation of blood occurs, and maternal erythrocytes can be detected within the cavities of the areolae and also within the trophoblast cells of the domes.

After the application of methyl-green and pyronin reagents the most intense staining reaction is obtained in the cytoplasm of the trophoblast. This intensity of staining is maintained throughout the period of vascular omphaloidean placentation and into late pregnancy. The cytoplasm of the trophoblast cells of the areolae, however, stains but faintly. A strong staining reaction is also obtained in the cytoplasm of the decidual tissue and in the distal cytoplasm of the epithelia of the uterine glands. An intense reaction, comparable to that of the trophoblast, is obtained in the cytoplasm of the endodermal epithelial cells of the vascular part of the yolk-sac. By the 5 mm. stage most of the endodermal cells of the vascular portion of the yolk-sac are cuboidal in form.

Stainable glycogen is absent from the maternal tissues of the uterus in all stages of pregnancy that were tested. By the 5 mm. stage a considerable amount of decidual tissue is present and it gives a negative reaction for glycogen with Best's carmine method and PAS reagents. The trophoblastic villi, the trophoblast cells of the areolae and the yolk-sac endoderm are also devoid of glycogen.

In later stages the cytoplasm of the decidual cells stains faintly pink after the application of PAS reagents and this reaction is saliva resistant. The substance contained in the cavities below the trophoblastic domes and in the lumina of the associated glands is stained intensely with the PAS reagents. Material with essentially the same staining properties, much of which is granular, is also present in the cytoplasm of the cells of the trophoblastic domes.

Lipoidal material is present in the trophoblast in early implantation stages when the attachment of the trophoblast is first being effected along the thickened antimisometrial walls of the uterus. This material which is finely granular, is mainly concentrated in the distal cytoplasm of the trophoblast cells, and is present in amounts comparable to that in the cytoplasm of the uterine and

glandular epithelia. Later in pregnancy, when the vascular omphaloidean placenta has been established, only a very slight staining reaction is obtained in the trophoblast of the villi which have been formed. An intense staining reaction with both Sudan black and osmic acid is obtained in that portion of the decidual tissue lying immediately adjacent to the trophoblast of the villi (Pl. 1, fig. D). This is the symplasma tissue which is derived from the uterine epithelium and forms a syncytial covering over the trophoblastic villi. The remainder, and by far the greater portion of the decidual tissue contains very little lipoidal material. The acid haematin method and pyridine extraction test reveal that no discernible amounts of phospholipid are present in the trophoblast or decidua.

In early implantation stages alkaline phosphatase is present in the epithelial cells and lumina of the uterine glands in amounts comparable to that in the oestrous uterus. Lesser amounts are present in the uterine epithelial cells. Some alkaline phosphatase is also present in the trophoblast of the implanting blastocyst (Pl. 1, fig. B). After the establishment of the vascular omphaloidean placenta the reaction obtained in the uterine glands is similar to that of early stages. The distribution of the enzyme in the tissues which comprise the vascular yolk-sac placenta is essentially similar to that in the newly formed allantochorionic placenta. As the allantoic mesoderm extends the tropoblastic villi become hollowed out and partially filled with mesenchyme, and it is at this stage that the distribution of alkline phosphatase can be seen most readily. The most intense reaction is obtained in the symplasma, derived from the uterine epithelium, which surrounds the villi, and a less intense reaction is obtained in the trophoblast of the villi. The adjacent decidual tissue gives only a faint reaction (Pl. 1, fig. C). A strong reaction is obtained in the distal cytoplasm of the trophoblastic cells of the domes, with a faint reaction in the cavities of the areolae.

After the application of Perl's method for ferric iron a faint reaction is obtained in the cytoplasm of the epithelial cells of the uterine glands and also in the lumina of the glands.

The avascular yolk-sac placenta

An avascular yolk-sac placenta is formed early in development by the initial attachment of the trophoblast of the blastocyst to the uterine epithelium of the thick lateral walls of the uterus. However, this is rapidly converted into a vascular placenta by the extension of the area vasculosa. An avascular yolk-sac placenta is also formed mesometrially and by the 3·5 mm. stage the attachment of the trophoblast to the uterine epithelium in this region is extensive. Since the mesoderm does not spread to any great extent beyond the sinus terminalis a large avascular segment of the yolk-sac persists throughout pregnancy.

The degenerative changes which occur in the uterine epithelium of the mesometrial region have been described by Vernhout (1895). In 5 mm. stages some intact epithelium is still present and the overall thickness of the tissues comprising the foetal portion of the placenta is of the order of 40 μ. At this stage the yolk-sac endoderm is squamous in form and the underlying

membrane of Reichert is very thin. Subsequently the yolk-sac endoderm thickens and becomes cuboidal ; Reichert's membrane becomes thicker and the trophoblast tissue becomes thicker and generally more compact. In 9 mm. stages the uterine epithelium has completely disappeared and the foetal tissues of the placenta form a band about 50–60 μ thick. In later stages this measurement increases due mainly to the growth of the trophoblast, so that in places the foetal part of the placenta is 100 μ thick (Pl. 2, fig. H). The placenta also becomes more extensive leading to a reduction in the size of the unattached zone of trophoblast.

Laterally, as seen in transverse sections, the trophoblast of the yolk-sac wall is not attached to the uterine epithelium. At the 5 mm. stage it is formed of a regular layer of columnar cells with basal nuclei. Later these cells increase in height and Reichert's membrane is present underlying them, and the cells of the yolk-sac endoderm are cuboidal in form (Pl. 3, fig. J). This unattached region of the yolk-sac wall, the relative extent of which is reduced in late pregnancy, can be considered as a part of the avascular yolk-sac placenta. By the 22 mm. stage the allantoic mesoderm has extended below the trophoblast of this unattached region (Pl. 3, fig. K), so that a vascular membrane is formed with occasional blunt villous-like structures projecting into the uterine lumen.

The cytoplasm of the trophoblast of the mesometrial wall of the blastocyst is stained intensely after the application of methyl-green and pyronin reagents, and this intense reaction is maintained after the attachment of this tissue to the uterine epithelium is effected. Throughout early pregnancy the trophoblast and the squamous endoderm of the avascular placenta is very rich in RNA, but in late stages there is a slight reduction in the staining reaction obtained in both tissues. A stronger staining reaction is obtained in the connective tissue of the mesometrial uterine wall of the pregnant uterus than in that of the non-pregnant uterus. The distal cytoplasm of the epithelia of the uterine glands associated with the avascular placenta is very rich in RNA, and the intensity of the staining reaction obtained in the glandular epithelia is maintained into very late pregnancy. A strong staining reaction is also obtained in the cytoplasm of the trophoblast and endoderm of the unattached region of the yolk-sac wall in early and late stages of pregnancy. The cytoplasm of the trophoblast in this unattached region does not stain as intensely as that of the trophoblast of the avascular placenta proper.

Discernible glycogen is absent from the tissues of the avascular placenta in all the stages that were treated with PAS reagents and Best's carmine stain. After the application of PAS reagents the staining reaction obtained in the trophoblast of the avascular placenta is not uniform. The finely particulate material which is present throughout the cytoplasm is stained a deep crimson colour, and in certain localities where this material is aggregated together a very intense staining reaction is obtained. These reactions are saliva resistant. The contents of some of the cavities which are present in the trophoblast are similarly stained. Granular material with similar staining properties is also present in the yolk-sac endoderm. The reactions described above were obtained in blastocyst stages, and in 5, 9 and 16 mm. stages.

In later stages of pregnancy there is a slight reduction in the intensity of the staining reactions obtained but considerable PAS positive material is still present in the tissues of the avascular placenta at the 29 mm. stage (Pl. 3, fig. L). Throughout pregnancy the distal cytoplasm of the cells of the uterine glands is very rich in PAS positive material, and the contents of the glands are also stained intensely by PAS reagents. Finely particulate PAS positive material is also present in considerable amount in the cytoplasm of the trophoblast cells of the unattached region of the yolk-sac wall, and the fluid contents of the uterine lumen which bathe this trophoblast are also stained deeply crimson by PAS reagents.

The presence of lipoidal material in the trophoblast and uterine epithelium in early implantation stages has been described. Subsequent to the attachment of the trophoblast to the uterine epithelium in the mesometrial region there is no marked increase in the amount of lipoidal material present. At the 10 mm. stage only a faint dusting of the cytoplasm of the trophoblast and endoderm of the avascular placenta occurs after the application of Sudan black —comparable to the results obtained in the epithelial cells of the uterine glands in this region and in the trophoblast cells of the unattached portion of the yolk-sac wall. In all the later stages of pregnancy that were treated with Sudan black and osmic acid similar results were obtained. Kull's method for mitochondria reveals the presence of strongly fuchsinophil material in the cells of the yolk-sac endoderm. By the 10 mm. stage these cells have become very much thicker and the rounded fuchsinophil droplets which vary in size, are mainly concentrated in the immediate vicinity of the nuclei, most frequently in a basal position. Elsewhere in the avascular placenta proper very little fuchsinophil material is present. In the cytoplasm of many of the cells of the unattached region of trophoblast, particularly in late stages of pregnancy, very large inclusions are present which stain intensely with acid fuchsin (Pl. 3, fig. M). The contents of the uterine lumen, which in late stages contains much cell debris derived mainly from the degenerating uterine epithelium, is also strongly fuchsinophil.

The distribution of alkaline phosphatase in the maternal and foetal tissues of early implantation stages has been described. Shortly after the attachment of the trophoblast to the mesometrial uterine epithelium the enzyme is present in considerable amounts in the yolk-sac endoderm, trophoblast and uterine epithelium. In later stages, after the application of Gomori's cobalt-calcium technique, a strong reaction is obtained in the trophoblast of the avascular placenta and this condition is maintained into very late pregnancy (Pl. 1, fig. E). A similar strong and persistant reaction is obtained in the epithelial cells of the mesometrial uterine glands and in the lumina of the glands. In late stages relatively little of the enzyme is present in the yolk-sac endoderm. Throughout pregnancy alkaline phosphatase is present in the distal cytoplasm of the cells of the unattached trophoblast, but the reaction obtained here is never as intense as that in the trophoblast of the avascular placenta proper.

The cytoplasm of the epithelia of the uterine glands is stained faintly blue after the use of Perl's method for ferric iron and a faint staining reaction is also obtained in the lumina of the glands.

Reichert's membrane

Strahl (1892) has described the formation of a membrane between the trophoblast and endoderm of the bilaminar wall of the yolk-sac. This membrane becomes thicker in late stages of pregnancy and persists to term.

The membrane first becomes discernible very early in pregnancy and can be detected in the bilaminar yolk-sac wall shortly after the completion of amniogenesis. In such early stages it is only 1 μ thick, at the 5 mm. stage it is generally less than 2 μ in thickness and extends throughout the bilaminar wall up to the margin of the area vasculosa. By the 16 mm. stage its thickness has increased generally to 3 μ and there is no apparent further increase in its thickness in very late pregnancy.

In *Talpa* the mesoderm has begun to extend beyond the sinus terminalis by the 5 mm. stage, and in so doing it separates the trophoblast from Reichert's membrane, the latter remaining in contact with the endoderm. The membrane in this region thickens as pregnancy proceeds, and it is not reformed below the trophoblast from which it has been separated by the mesoderm (Pl. 3, fig. K). The mesoderm never completes its extension mesometrially so that a large bilaminar segment of the yolk-sac persists to term. Subsequently the exocoel extends up to the limit of the mesoderm.

Throughout pregnancy, Reichert's membrane is stained intensely green by Masson trichrome stain, and bright red by Lillie's allochrome method for connective tissue (1951). It is stained readily by eosin and orange G and in Azan preparations it is stained a deep blue colour in all stages of pregnancy. Weigert's resorcin fuchsin for elastic tissue leaves the membrane essentially unstained, whereas it stains readily with Van Gieson's stain for collagen.

In frozen sections stained with Sudan black, Reichert's membrane is completely unstained. Similarly, in material fixed in Champy's fluid and post-osmificated for varying periods, the membrane is unaffected.

The PAS reagents stained Reichert's membrane a crimson colour in all the stages of pregnancy that were tested. This reaction is saliva resistant and the intensity of staining is similar throughout its entire extent (Pl. 3, fig. L). Gomori's silver method for the impregnation of reticulum (Gomori, 1937), impregnates the membrane in all the stages of pregnancy to which the technique was applied. The membrane is stained uniformly black throughout its extent.

In stained and unstained sections of early and late stages of pregnancy cut from blocks which had been fixed in either Bouin's, Rossman's, Zenker's or Champy's fixative, Reichert's membrane does not exhibit birefringence. In deparaffinized and frozen sections of late stages of pregnancy which had been fixed in formalin the membrane exhibits faint birefringence.

The yolk-sac splanchnopleur

At the 5 mm. stage the vitelline circulation is adjacent to the thickened uterine mucosa only over a limited extent and in such stages the endoderm of the vascular segment of the yolk-sac is cuboidal in form. The limit of the area vasculosa is marked by a large sinus terminalis. In later stages the endodermal cells of the yolk-sac splanchnopleur become columnar and their convex

apical ends are surmounted by a brush border of short closely set hairs. Throughout pregnancy the membrane is highly vascular and in late stages it becomes much folded. The larger vitelline vessels with their endoderm and mesenchyme coverings protrude into the yolk-sac cavity. Finely particulate granular material is present in the distal cytoplasm of the endoderm particularly in the later stages of pregnancy. This material is usually stained an orange colour by the Azan method and is eosonophilic. The granules are stained faintly green after the use of Masson's trichrome stain.

In 5 mm. stages a strong reaction for RNA is obtained in the cytoplasm of the endodermal epithelium of the membrane, comparable in intensity to that in the trophoblast. This intense staining reaction is maintained throughout the early stages of pregnancy but by the 16 mm. stage, and in subsequent stages, the amount of RNA in these cells is considerably reduced.

Discernible glycogen is absent from the membrane in all the stages of pregnancy that were tested. At the 5 mm. stage the cytoplasm of the endodermal epithelium is stained faintly pink after the application of PAS reagents, and the intensity of this reaction has increased by the 9 mm. stage. In subsequent stages there is no marked increase in the amount of this granular PAS positive material in the endoderm of the membrane.

In early stages of pregnancy a faint dusting of the cytoplasm of the endoderm results after the use of Sudan black. A heavier dusting occurs in these cells in later stages of pregnancy but no distinct lipoidal droplets can be discerned within the cells. Similar results were obtained in Champy fixed material, some of which was post-osmificated. Kull's method for mitochondria reveals the presence of minute rounded bodies in the distal cytoplasm of the endodermal cells in all stages of pregnancy. As pregnancy proceeds, the mesoderm slowly extends beyond the sinus terminalis and becomes vascularised. The marginal area of the yolk-sac splanchnopleur which is formed in this way is therefore composed of endoderm which was previously a part of the avascular segment of the yolk-sac and which now overlies vascular splanchnic mesoderm. The rounded fuchsinophil droplets, the presence of which in the endoderm of the avascular placenta has been described, can be seen in the endodermal cells of this marginal zone of the yolk-sac splachnopleur. However, the columnar endoderm of the membrane does not contain this material.

A moderate reaction for alkaline phosphatase is obtained in the cytoplasm of the endoderm at the 9 mm. stage. The enzyme is also present in the yolk-sac lumen adjacent to the endoderm and there is no marked increase in the amount of the enzyme in these sites in later stages of pregnancy.

No positive reactions for iron were obtained in the tissues of the membrane in all the stages of pregnancy that were tested.

The yolk-sac fluid

The presence of a coagulum is noticeable in the yolk-sac cavity in sections of early blastocyst stages. In such early stages it appears dispersed evenly throughout the cavity, but in later stages it is usually much more concentrated around the periphery of the yolk-sac. By the 16 mm. stage the growth of the embryo has caused the invagination of the vascular yolk-sac splanchnopleur

into the yolk-sac cavity and in later stages of pregnancy the yolk-sac appears crescentic in shape in transverse sections. In such stages a dense coagulum is present throughout the cavity.

The staining properties of the contents of the yolk-sac are consistant throughout pregnancy. The staining reactions obtained in late stages are more intense due to the increased concentration of the coagulum. The flocculent protein material contained in the yolk-sac shows a marked affinity for acid dyes. After Zenker fixation and the application of Masson's trichrome stain the flocculent precipitate in the yolk-sac is stained a reddish brown colour and in certain regions this reddish-brown precipitate is embedded in a green stained matrix. The precipitate stains readily with eosin and is stained an orange colour by the Azan method. The contents of the uterine lumen are stained similarly, particularly in the later stages of pregnancy. In early pregnancy the yolk-sac coagulum is stained faintly pink after the application of PAS reagents. In later stages of pregnancy a deep crimson colour is obtained. These reactions are saliva resistant.

Table 1 shows the concentration of protein nitrogen in the maternal sera of one non-pregnant and six pregnant females ; and the concentration in the yolk-sac fluid of eleven females at different stages of pregnancy.

TABLE 1

The yolk-sac fluid and maternal serum of the mole

Animal number	Stage of pregnancy (Crown-rump length of embryo in mm.)	Average wt. in gm. of contents of a single yolk-sac	Conc. of protein nitrogen (mg./ml.)		Reaction with Thrombin
			* Yolk-sac fluid	† Maternal serum	
M.31	Non-pregnant	..	..	9·17	..
M.34	Early Blastocyst	0·018	0·47	9·20	—
M.48	Blastocyst	0·027	..	..	..
M.33	Late Blastocyst	0·044	0·50	..	—
M.32	3·5	0·060	0·53	..	—
M.21	3·5	0·058	..	8·50	..
M.54	4	0·083	..	..	—
M.50	5	0·084	0·60	9·38	—
M.45	9	0·095	3·78	..	—
M.44	11·5	0·129	5·74	..	—
M.51	12·5	0·077	9·03	..	—
M.30	16	0·075	12·6	9·31	—
M.47	19	0·047	14·2	..	—
M.11	20	0·049	14·4	8·33	—
M.14	24	0·036	14·6	..	—
M.53	29	0·028	..	8·33	—

* The mean of at least six determinations in which the variation was not greater than ±1 per cent of the arithmetic mean.

† The mean of three determinations in which the variation was not greater than ± 1 per cent of the arithmetic mean.

In early blastocyst stages of pregnancy it is probable that the yolk-sac fluid samples that were collected included some part of the contents of the amniotic cavity since complete separation of the two fluids is particularly difficult in these stages. As pregnancy proceeds the volume of the yolk-sac increases, and it continues to increase up to about the 11·5 mm. stage. The concentration of protein nitrogen in the yolk-sac fluid also increases and by the 11·5 mm. stage is approximately 60 per cent of that in the maternal serum. There is a very marked increase in the concentration within the yolk-sac between the 5 mm. and 9 mm. stages at which time the vascular segment of the yolk-sac wall is being separated from the trophoblast of the chorion. The vascular yolk-sac placenta is of very limited extent at the 5 mm. stage and this process of separation is completed shortly before the 9 mm. stage.

After the 11·5 mm. stage the volume of the yolk-sac diminishes but the concentration of protein nitrogen continues to increase. At the 12·5 mm. stage the concentration is 9·03 mg./ml. and this increase in concentration could be accounted for by the absorption of water from the yolk-sac. In later stages the concentration in the yolk-sac fluid is higher than that in the maternal serum and it is probable that there is a continual entry of protein into the yolk-sac in late pregnancy. After the 19 mm. stage there is no further large increase in the concentration ; and in such stages it is difficult to dissect out cleanly the frozen yolk-sac fluid from the conceptus. Care was taken to avoid contamination with maternal blood. The fluid obtained from these late stages is similar in colour to the maternal serum. In all the stages of pregnancy in which the yolk-sac fluid was tested for the presence of fibrinogen negative results were obtained.

DISCUSSION

In *Talpa europaea* a vascular omphaloidean placenta is formed in early pregnancy over the thickened antimesometrial wall of the uterus. At the 5 mm. stage the vascular segment of the yolk-sac is in contact with the uterine tissue only over a very limited extent and by the 9 mm. stage vascular omphaloidean placentation has been terminated. This placenta is of the endotheliochorial type and the trophoblastic villi which are formed are not vascularised by the vitelline circulation. It is therefore far less vascular than that which is formed in *Erinaceus* (Morris, 1953), and no intimate apposition of the maternal and foetal circulations is effected within it.

The conversion of subepithelial connective tissue into decidual tissue is accompanied, as in *Erinaceus*, by an increase in the amount of RNA, but glycogen is not formed in the decidua of *Talpa*. Lipoid material is not present in any great amount except in that portion of the decidua which forms a syncytial covering over the trophoblastic villi and which is derived from the uterine epithelium. Some lipoidal material is present within the trophoblast cells of the villi. Similarly alkaline phosphatase is present in this syncytial layer with considerably smaller amounts present in the trophoblast and the remainder of the decidua. The vascular yolk-sac placenta may therefore be of some importance in the uptake of lipoidal material from the maternal blood and the alkaline phosphatase in these tissues may be involved in this

mechanism (Bloor, 1943). The importance of the placenta in this connection is not comparable with that in *Erinaceus* where the placenta is highly vascular and the amount of lipoidal material present in its tissues is very considerably greater (Morris, 1957). Since in *Talpa* the trophoblastic villi remain avascular during the phase of omphaloidean placentation, any absorption which may occur must follow a cell-to-cell path. It is evident that the structural changes which occur in the uterine wall during this phase are essentially preparatory to the subsequent establishment of the allantochorionic placenta with highly vascular foetal villi. The distribution of RNA, lipoids and alkaline phosphatase in the newly formed allantochorionic placenta is essentially the same as in the omphaloidean placenta, but in the former the total absorptive surface is continually increasing and the vascularisation of the mesodermal cores of the villi rapidly ensues. The absorptive mechanism is thus rendered far more efficient.

The persistance of certain of the uterine glands in the region of the vascular yolk-sac placenta has been noted. The aerolae which are formed in association with these glands are very similar in form to those which have been described in a wide variety of species (Amoroso, 1952). In *Talpa* they are first formed during the phase of vascular omphaloidean placentation and persist into late pregnancy. The columnar trophoblast cells, which are arranged to form a dome-like structure, are closely associated with vessels of the vitelline circulation. These structures are absorptive in function and are concerned in the uptake of the secretions of the glands with which they are associated. The secretions stain intensely with PAS reagents and particulate material with similar staining properties is present within the trophoblast cells. Alkaline phosphatase is present in the glandular epithelia, the lumina of the aerolae and in the trophoblastic domes. Maternal erythrocytes, derived from the extravasations which occur near the sites of the aerolae, can be seen within the columnar trophoblast cells. These aerolae, associated first with the vitelline circulation and later with the allantoic circulation, are probably important sites for the entry into the foetal tissues of iron, saliva insoluble carbohydrate material—probably mucoprotein or mucopolysaccaride, and other substances contained in the secretions of the glands.

The mechanism of implantation in *Talpa europaea* involves the disruption and eventual degeneration of most of the uterine epithelium of the mesometrial portion of the uterus (Vernhout, 1895). The manner in which the initial attachment of the trophoblast is effected in this region is similar to that in the rabbit in which the uterine epithelium is sloughed off at about nine to nine-and-a-half days and degenerates. In rabbit a new uterine epithelium is regenerated from the epithelial elements of the uterine glands and the degenerating uterine epithelium has been compared with the decidua capsularis of other forms (Morris, 1950). In *Talpa* there is no subsequent regeneration of the uterine epithelium, and the tendency for this tissue to degenerate is apparent even in those restricted regions in which the trophoblast is not in contact with the uterine tissues. The trophoblast is thus brought into contact with the sub-epithelial connective tissue and generally is in the form of an irregular double layer in which are numerous fluid filled cavities. The progressive

thickening of the foetal tissues of the avascular placenta has been described, and there is no penetration of the sub-epithelial connective tissue by the trophoblast.

The avascular placenta formed in this way is concerned in the absorption of substances produced by the uterine glands of the narrow mesometrial region of the uterine wall. These glands open, by means of short ducts, into spaces contained in the trophoblast. The staining reactions obtained in the tissues of this placenta after the use of PAS reagents indicate that it is concerned in the uptake of saliva insoluble carbohydrate material secreted by the uterine glands. Throughout pregnancy the uterine secretions contain much PAS positive material and the staining reactions of the yolk-sac fluid indicate that similar material is present within it. Glycogen is absent from the placental tissues and from the glandular epithelia and relatively little lipoidal material is present within the trophoblast.

In early stages of pregnancy when the volume of the yolk-sac is increasing, it is dependant for any renewal of its fluid contents on substances which enter it either via the vascular or avascular yolk-sac placentae. In such stages the allantoic circulation is not fully established and the absorptive surface afforded by the vascular placenta is being very rapidly reduced, whereas that of the avascular placenta is being extended. These factors, together with the avascular nature of the trophoblastic villi, strongly suggest that it is the avascular yolk-sac placenta and the associated unattached wall of the blastocyst which are of special significance in *Talpa*. The subsequent transmission into the yolk-sac cavity of substances which have been absorbed via this route involves passage through Reichert's membrane—conditions similar to those which have been described in the rat (Everett, 1935). During early pregnancy the concentration of protein nitrogen in the yolk-sac cavity is relatively low, but subsequently between 5 mm. and 11·5 mm. stages the concentration increases considerably. This increase in concentration occurs initially when vascular omphaloidean placentation is being terminated and the allantochorionic placenta is not fully established. It is therefore probable that the avascular placenta is involved in the uptake of amino acid or protein from the uterine secretions and that this material—at least in part—passes into the yolk-sac cavity. The ability of trophoblast to absorb substances of large molecular size, particularly in early pregnancy, is well known, and in many species this activity is of importance in the nutrition of the early embryo (Huggett & Hammond, 1952). The increased protein concentration within the yolk-sac can be correlated with the progressive establishment of the avascular placenta. The columnar trophoblast cells of the unattached portion of the yolk sac wall, the histochemical properties of which have been described, also serve an absorptive function. They are in contact with the uterine secretions and their histochemical properties indicate that they are probably active, possibly to a lesser degree, in the uptake of material similar to that which is absorbed by the trophoblast of the avascular placenta. In later stages the vascular allantoic mesoderm extends below these cells converting a part of the membrane into a vascular structure, and occasionally blunt villous-like prominences develop upon it. Throughout pregnancy alkaline phosphatase

is present in the cytoplasm of these trophoblast cells but never in amounts comparable to that in the trophoblast of the avascular placenta proper.

Whereas in the rabbit there is a rapid build up in the concentration of protein in the yolk-sac cavity between seven and nine days *post coitum*, reaching as high as 40 to 50 per cent of that in the maternal blood (Brambell & Hemmings 1949), in *Putorius furo* and *Erinaceus europaea* there is no such comparable build up. Fibrinogen, of maternal origin is present in the yolk-sac of the rabbit in seven, eight and nine day stages whereas it is absent from the yolk-sac fluid of *Putorius* and only appears in that of *Erinaceus* in very late stages of pregnancy in which it is considered to be of foetal origin (Morris, 1953). Fibrinogen was absent from the yolk-sac fluid of *Talpa* in all the stages of pregnancy that were tested, but in this species a build up in the concentration of protein in the yolk-sac fluid, comparable with that in rabbit, does occur relatively later in pregnancy. In this species there is no close association between the maternal circulation and the trophoblast during early pregnancy similar to that which has been described for the rabbit and hedgehog. The vascularity of the mesometrial uterine wall is increased during pregnancy but in *Talpa* it is the secretory activity of the uterine glands which is of significance as a source of protein material at least in the first half of pregnancy. In later stages, following the full establishment of the allantochorionic placenta, proteins and other substances absorbed at this placental site may enter the yolk-sac cavity by way of the foetal circulation and the yolk-sac splanchnopleur. The high concentration of protein in the yolk-sac in late pregnancy, could be due, in part, to the absorption of water from the cavity. However, the histochemistry of the foetal and maternal tissues suggests that the absorptive activity of the avascular placenta continues during later pregnancy, contrasting with the conditions described in *Erinaceus* in which the avascular yolk-sac is of little importance as a placental structure in later pregnancy (Morris, 1957). In late stages of pregnancy in *Talpa* the trophoblast of the avascular placenta is rich in alkaline phosphatase whereas little of this enzyme is present in the corresponding tissue in *Erinaceus*.

Discernible glycogen and iron are absent from the endodermal epithelium of the yolk-sac splanchnopleur in all the stages of pregnancy that were tested, but some PAS positive saliva insoluble material is present within the cells from the 5 mm. stage onwards. A moderate reaction with Gomori's cobalt-calcium method for alkaline phosphatase is obtained in these cells for the greater part of pregnancy, and this enzyme is also present in the yolk-sac fluid adjacent to the endoderm of the yolk-sac wall. Granular material, the staining properties of which have been described, is present in the cytoplasm of the endoderm in increasing amounts as pregnancy proceeds. The granular material present in the endoderm of the yolk-sac splanchnopleur of rodents has been described by various authors (Branca, 1923 ; Bridgman, 1948 ; Morris, 1950 ; Wislocki *et al.*, 1946) and opinion has varied as to whether these granules are secretory or whether they are absorption products. The presence of a brush border on the endodermal cells of the membrane in *Talpa* would seem to favour the theory that these cells are mainly concerned in absorption, their histochemical

properties suggesting that some saliva insoluble carbohydrate material is being absorbed from the yolk-sac fluid.

As development proceeds the enlargement of the embryo causes the partial invagination of the yolk-sac splanchnopleur and the yolk-sac cavity is reduced in size. Throughout pregnancy the membrane is in contact with the fluid content of the yolk-sac. In *Erinaceus* there is evidence that the highly vascular omphaloidean placenta is of considerable importance as a placental structure in early pregnancy, and that substances which are absorbed at this placental site from the maternal blood pass into the foetal blood, and are not transmitted to any large extent into the yolk-sac cavity (Morris, 1957). It is apparent that in *Talpa*, however, substances which are absorbed by the avascular yolk-sac wall from the uterine secretions are transmitted, at least in part, into the yolk-sac cavity. The yolk-sac fluid in this species could therefore serve as an important source of absorbable material. The endoderm of the yolk-sac splanchnopleur of the rabbit is readily permeable to immune globulin prepared in rabbits and since antibody activity depends on the surface configuration of the molecules any considerable alteration of the molecule is liable to destroy its immunological activity (Brambell, 1954). There is also evidence of the uptake of antibody by the membrane in the rat (Brambell & Halliday, 1956). Thus in the only mammalian species investigated there is experimental evidence that the endoderm of the yolk-sac splanchnopleur is capable of absorbing unaltered protein, and it has been suggested that such activity may occur in other forms in which the yolk-sac is inverted and the yolk-sac splanchnopleur is exposed to the contents of the uterine lumen. This may well be a property of the membrane in species with a closed yolk-sac in which event protein material transmitted into the yolk-sac cavity, as in *Talpa*, may be made available to the foetus.

It is evident from the foregoing discussion that the uterine secretions in *Talpa* are of importance in embryonic nutrition, and that they may continue to be of significance even in late pregnancy. Glycogen and iron are absent from the endometrium of the oestrous female and in pregnant uteri only faint positive reactions were obtained in the uterine glands after the application of Perl's method for ferric iron. Throughout pregnancy the glandular epithelia are rich in RNA—a substance important in protein synthesis (Danielli, 1953) —and contain more lipoidal and considerably more PAS positive material than in *Erinaceus* (Morris, 1957). Alkaline phosphatase is present in the epithelia and in the lumina of the glands throughout pregnancy.

Reichert's membrane is formed in the avascular wall of the yolk-sac in early stages of pregnancy. In such stages it is about 1 μ thick, but by the 16 mm. stage it has generally attained a thickness of about 3 μ. In early stages it is located exclusively between the endoderm and trophoblast of the yolk-sac wall, extending almost up to the margin of the sinus terminalis. The subsequent extension of the mesoderm beyond the sinus terminalis separates the membrane from the trophoblast, so that it comes to lie between the endoderm and the extending mesoderm. In this region the membrane thickens as pregnancy proceeds and is comparable in thickness, in all stages of pregnancy, to the membrane elsewhere in the yolk-sac wall. There is no subsequent

reformation of the membrane beneath the trophoblast from which it has been removed by the extending mesoderm. Throughout its extent, and in all stages of pregnancy, it is in contact with the yolk-sac endoderm. This contrasts markedly with the conditions which have been described in *Erinaceus* (Morris, 1953), in which the membrane is of trophoblastic origin. The membrane which is formed in the Common and Lesser shrews (Brambell & Perry, 1945) is considered to be of trophoblastic origin, whereas in the rat and mouse its origin is uncertain. In *Talpa* the membrane is probably derived from the endoderm with which it is in contact throughout pregnancy. It is unlikely that the trophoblast contributes to its formation since it is not reformed below this tissue, from which it is separated by the extending mesoderm in early stages of pregnancy.

The histochemical and tinctorial reactions of the membrane have been described. They are very similar to those which have been described in the rat (Wislocki & Padykula, 1953), and in *Erinaceus* (Morris, 1957). The membrane is of uniform thickness throughout its extent and is strongly PAS positive in all stages of pregnancy indicating that it contains some mucoploysaccharide or glycoprotein. Its properties indicate that, as in the rat and hedgehog, it is formed of collagenous material.

SUMMARY

1. The distribution of RNA, fats, iron, glycogen and alkaline phosphatase in the endometrium, yolk-sac placenta and decidua of *Talpa europaea* is described.

2. The *areolae* which are formed are associated, at first, with the vitelline circulation and are probably important sites for the uptake of iron—derived from maternal erythrocytes, protein and saliva insoluble carbohydrate material derived from the secretions of the adjacent uterine glands. The aerolae persist into late pregnancy in association with the allantoic circulation.

3. A vascular yolk-sac placenta is formed in early pregnancy but it is probably not of any real significance in embryonic nutrition—with the exception of the areolae mentioned above. It is evident that the structural changes which occur in the uterine wall during the formation of this placenta are essentially preparatory to the subsequent establishment of the allantochorionic placenta.

4. Stainable glycogen is absent from the decidual tissue and little lipoidal material is present except in the symplasma which invests the trophoblastic villi.

5. The avascular yolk-sac placenta, the progressive establishment of which is described, is concerned with the absorption of protein, saliva insoluble carbohydrate material and other substances contained in the secretions of the uterine glands of the mesometrial wall of the uterus. The uterine secretions are of considerable importance in embryonic nutrition and probably continue to be of some significance even in late pregnancy.

6. The yolk-sac increases in volume up to about the 11·5 mm. stage and the concentration of protein in its fluid at this stage is about 60 per cent of that in the maternal serum. In late stages the concentration of protein in the fluid is greater than that in the maternal serum. Fibrinogen is absent from the fluid in *Talpa*.

7. The yolk-sac fluid could serve as an important source of absorbable material and it is probable that the yolk-sac splanchnopleur, the histochemical and histological properties of which are described, is of some significance as a placental structure in this species.

8. Reichert's membrane is formed in the avascular wall of the yolk-sac in early pregnancy and it attains a thickness of about 3 μ in late stages. Its histochemical and tinctorial properties resemble those which have been described for the membrane in the rat and hedgehog and, as in these species, it is formed of collagenous material. In *Talpa* the membrane is probably of endodermal origin.

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EXPLANATION OF PLATES

PLATE 1

Fig. A. Part of a transverse section of the uterus of an oestrous female showing the presence of alkaline phosphatase in the uterine epithelium, glandular epithelium and lumina of the uterine glands. Cold acetone fixation.

,, B. Part of a transverse section of an early implantation site. Alkaline phosphatase, in considerable amount, is present in the uterine glands and trophoblast. Relatively little of the enzyme is present in uterine epithelium. Formalin fixation.

,, C. Part of a transverse section of the newly formed allantochorionic placenta. The trophoblastic villus has become hollowed out and partially filled with mesenchyme. Alkaline phosphatase is present in the symplasma investing the villus, with lesser amounts in the remainder of the decidua and trophoblast. Formalin fixation.

,, D. A section of a villus showing the lipoidal material present in the symplasma. Lesser amounts are present in the trophoblast and relatively little in the decidual tissue. Champy fixation and post-osmification.

,, E. A part of the avascular yolk-sac placenta of very late pregnancy. A considerable amount of alkaline phosphatase is still present in the trophoblast. Formalin fixation.

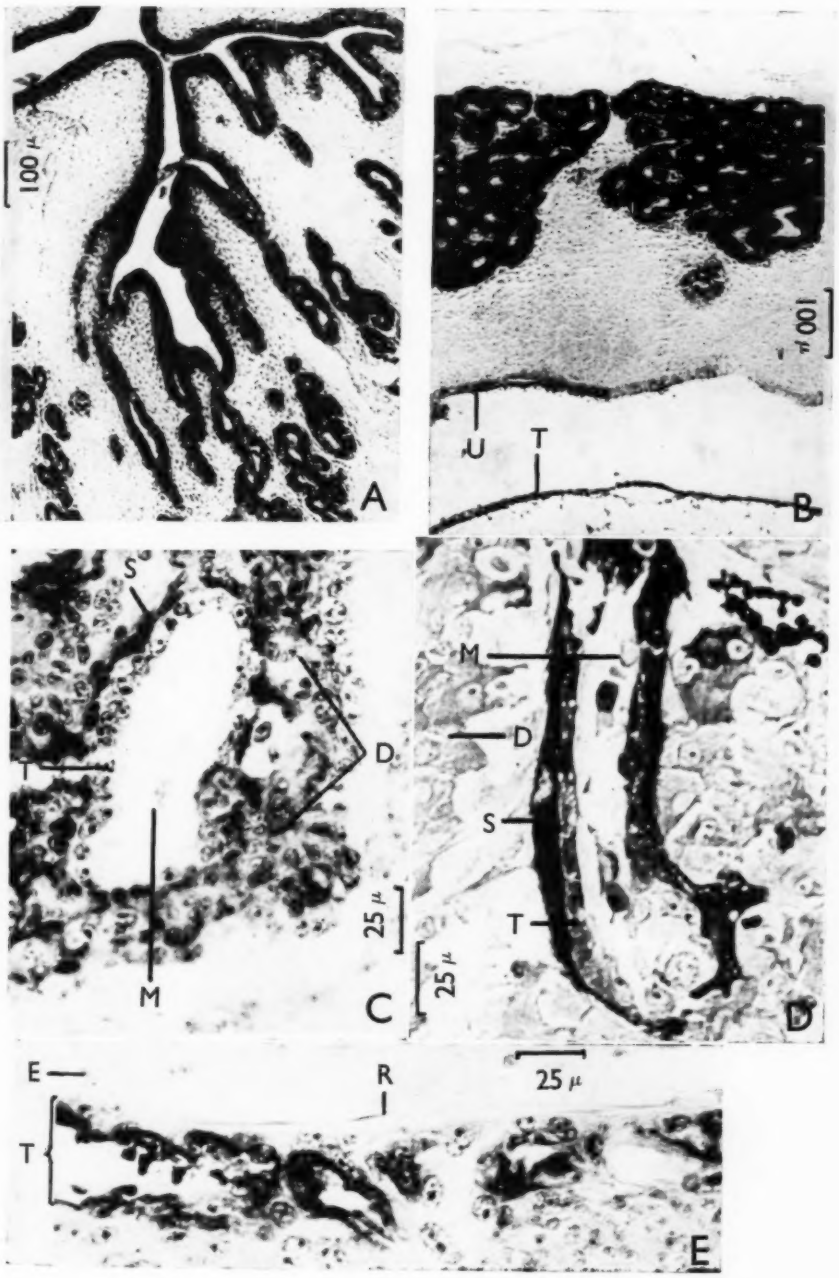
PLATE 2

Fig. F. A part of the vascular omphaloidean placenta showing the trophoblastic dome of an areola associated with the vitelline circulation. A heavily stained secretion is present within the cavity and maternal erythrocytes can be seen within the trophoblast cells of the dome. Bouin fixation and stained by Azan method.

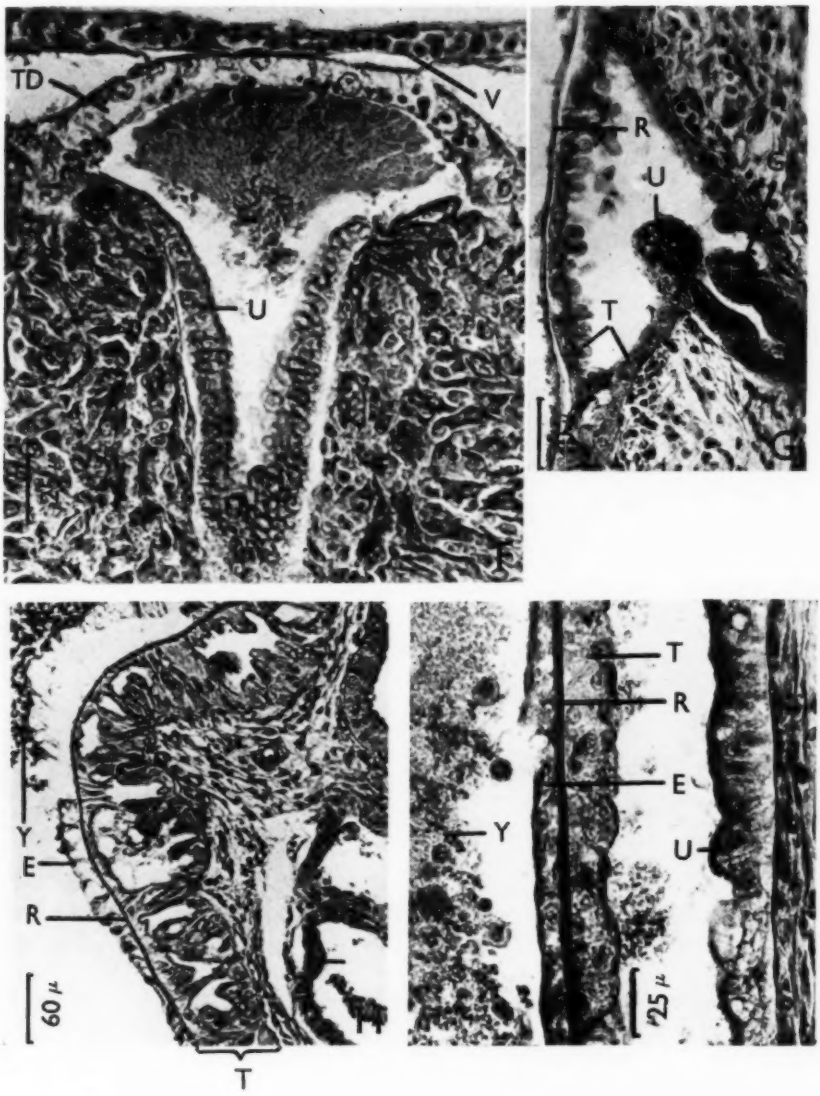
,, G. A part of the mesometrial wall of the conceptus showing the extension of the trophoblast below the glandular epithelia. In this region the uterine epithelium has degenerated and the glandular epithelium is being separated from the subepithelial tissue. Bouin fixation and stained by the Azan method.

,, H. A part of the avascular yolk-sac placenta at the 16 mm. stage showing the irregular double layer of trophoblast and Reichert's membrane. A heavily stained coagulum is present in the yolk-sac cavity and a coagulum with similar staining properties is observed in the lumina of the uterine glands. Zenker fixation and stained by the Azan method.

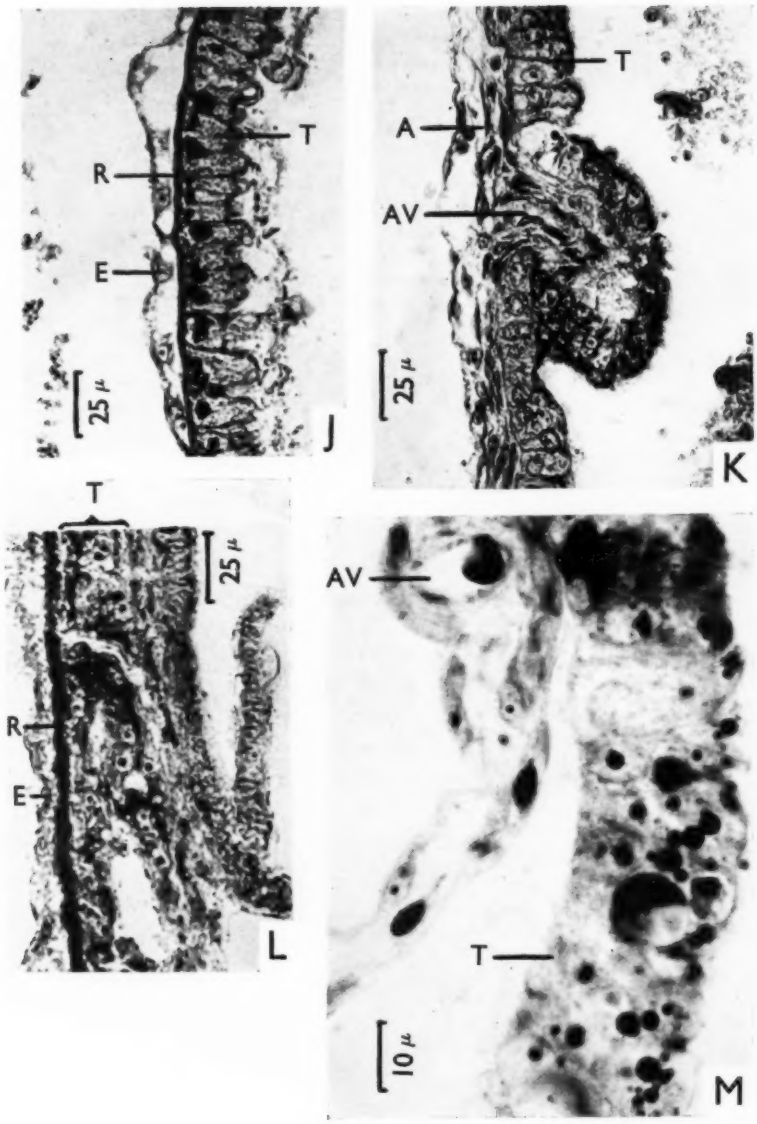
,, I. A part of a transverse section of a late conceptus showing the bilaminar yolk-sac wall and the degenerate appearance of a portion of the uterine epithelium in a region where the attachment of the trophoblast and uterine epithelium has not been effected. Bouin fixation and stained by the Azan method.



The yolk-sac of the mole *Talpa europaea*



The yolk-sac of the mole *Talpa europaea*



The yolk-sac of the mole *Talpa europaea*

Plate 3

Fig. J. A part of the unattached bilaminar wall of the yolk-sac at the 16 mm. stage showing the columnar cells of the trophoblast and the underlying membrane of Reichert. Zenker fixation and stained by the Azan method.

„ K. A part of the unattached region of trophoblast in a very late stage of pregnancy. Vascular allantoic mesoderm has now extended below this trophoblast and a villous-like structure has been formed on this portion of the membrane. The coagulum in the uterine lumen contains much cellular debris. Bouin fixation and stained with haematoxylin and eosin.

„ L. A part of the avascular yolk-sac placenta at the 29 mm. stage. Considerable PAS positive material is present in the trophoblast and Reichert's membrane is stained intensely crimson. Rossman fixation and PAS reagents after treatment with saliva.

„ M. A part of the unattached trophoblast in very late pregnancy. Large fuchsinophil droplets are present in the trophoblast. Helly fixation, post-chromed and stained with Kull's triple stain.

Abbreviations :

A.	Allantoic mesoderm	M.	Mesenchyme	TD.	Trophoblastic dome
AV.	Allantoic vessel	R.	Reichert's membrane	Y.	Uterine epithelium
D.	Decidua	S.	Symplasma	V.	Vitelline vessel
E.	Endoderm	T.	Trophoblast	Y.	Yolk-sac coagulum
G.	Glandular epithelium				

THE COMPARATIVE ETHOLOGY OF GRASSFINCHES (ERYTHRURAE) AND MANNIKINS (AMADINAE)

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(With 5 plates)

CONTENTS

	Page
Introduction	389
Geographical distribution	393
Morphology	395
Ethology	399
Agonistic behaviour	399
Nesting behaviour	401
Sexual behaviour	402
Parental behaviour	429
Comparative derivational problems	429
Discussion	432
Conclusion	435
Summary	436
Acknowledgments	437
References	437
Explanation of Plates	438

INTRODUCTION

This report is based on a laboratory study involving 263 estrildine finches, eighty-four of which were bred during the course of the investigation. A total of twenty-seven species of this subfamily (Estrildinae) of the Ploceidae came under observation at one time or another during the period of the study, which extended from the winter of 1951 to the spring of 1956.

The Estrildinae have been divided into three tribes by Delacour (1943): the waxbills (Estrildae), the grassfinches (Erythrurae) and the mannikins (Amadinae). The first of these three will not be dealt with in any detail here. Only twenty-five waxbills, belonging to six different species, were involved in the present investigation. Their behaviour was only briefly scrutinized. More attention was paid to the 130 grassfinches (belonging to ten species) and the 108 mannikins (belonging to eleven species) that were used.

A number of papers have already been published on various aspects of estrildine ethology (e.g. Morris, 1954 a, b; 1955 a, b, c, d, e; 1956 a, b; 1957 a, b; also see, Moynihan & Hall, 1954). These papers render an elaborate introduction superfluous here. For details of the observational techniques used, the reader is referred in particular to Morris, 1957 b.

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It is the aim of the present paper to bring together, in concise a form as possible, all the ethological data available for this group of birds and, with this material, to re-examine the taxonomy of the group.

The most recent and most comprehensive systematic arrangement for the estrildines is that provided by Delacour (loc. cit.). It is necessary to summarise this here, before proceeding further. It involves rather drastic changes, In many respects, from the earlier classifications. In recognizing only fifteen genera, with a total of 108 species, Delacour abandons as many as thirty-five old genera and twenty-nine species. Also, certain of the popular names he uses are not those normally employed. Whilst this radical nomenclatural upheaval produces considerable confusion in any discussion of the group and its members, it nevertheless should not be ignored (as it has been by certain recent authors). For Delacour's system, although it will be criticised in respect of certain details below, presents the first really unified estrildine classification. It sweeps away many unnecessary specific distinctions and simplifies the general picture considerably.

Delacour's arrangement

A. Waxbills (Estrildae)

Nine genera, with fifty-one species. Typified briefly as follows : Nestling palates marked with spots ; voice high-pitched ; vocalise with beak pointing upwards ; male often holds grass in beak during courtship dance ; more elegant and active than other estrildines ; predominantly Ethiopian.

The species will not be listed here, but the names of the few employed in the present study are 1, *Estrilda senegala* (Red-billed Fire-finch). 2, *E. angloensis* (Cordon Bleu). 3, *E. troglodytes* (Red-eared Waxbill). 4, *E. temporalis* (Red-browed Finch). 5, *E. melpoda* (Orange-cheeked Waxbill). 6, *E. amandava* (Red Avadavat).

B. Grassfinches (Erythrurae)

Three genera with twenty-three species. Typified as follows : Intermediate between waxbills and grassfinches—palate markings being nearer to waxbills, but voice unmelodious, like mannikins ; in courtship " the cock sits still, the flank feathers puffed out, the neck extended vertically and the beak turned downward, while he emits, apparently by a great effort, a kind of melody, sometimes inaudible. At the same time, he raises himself up and down with a lateral twisting " ; members of one genus (*Zonaeginthus*) include grass-offering ; generally clumsier than waxbills, but not so much so as mannikins ; predominantly Australasian.

Genus *Zonaeginthus*
Subgenus *Zonaeginthus*
Z. pictus (Painted Finch).
[*Z. oculatus* (Red-eared Fire-tail Finch).]
[*Z. bellus* (Fire-tail Finch).]
Z. guttatus (Diamond Sparrow).
Subgenus *Oreostruthus*
[*Z. fulginosus* (Crimson-bellied Mountain Finch).]

Genus *Poephila*
Subgenus *Neochmia*
P. phaeton (Crimson Finch).
P. ruficauda (Star Finch).
P. guttata (Zebra Finch).
P. bichenovi (Bicheno Finch).
[*P. modesta* (Cherry Finch).]
Subgenus *Poephila*
P. cincta (Parson Finch).
P. acuticauda (Long-tailed Grassfinch).
P. personata (Masked Grassfinch).
P. gouldiae (Gouldian Finch).
Genus *Erythrura*
(This genus, the Parrot Finches, comprises nine species. They will not be listed here, since little is known about them and none was included in the present study.)

C. Mannikins (Amadinae).
Genus *Padda*
P. oryzivora (Java Sparrow).
[*P. fuscata* (Timor Sparrow).]
Genus *Amadina*
A. fasciata (Cutthroat Finch).
[*A. erythrocephala* (Red-headed Finch).]
Genus *Lonchura*
Subgenus *Heteromunia*
L. pectoralis (Pectoral Finch).
Subgenus *Euodice*
L. malabarica (Silverbill).
[*L. griseicapilla* (Grey-headed Silverbill).]
Subgenus *Lonchura*
[*L. fringilloides* (Magpie Mannikin).]
L. bicolor (Black-breasted Mannikin).
L. cucullata (Bronze Mannikin).
L. striata (Striated Finch).
L. punctulata (Spice Finch).
[*L. nana* (Bib Finch).]
(This subgenus also contains seven other species about which so little is known that they will not be listed here.)
Subgenus *Munia*
L. ferruginosa (Chestnut Mannikin).
L. maja (Pale-headed Mannikin).
L. castaneothorax (Chestnut-breasted Mannikin).
(This subgenus also contains eleven other species about which so little is known that they will not be listed here. They are all island forms from the archipelago stretching from India to Australia, as are the seven unlisted species from the subgenus above.)

The above list requires some brief explanatory comments. Firstly, those species which were not studied in the present investigation are enclosed in square brackets. Secondly, although all the latin names given are exactly as put forward by Delacour, a few of the popular names have been adjusted to suit general usage. Where several old species have been merged into one by Delacour it has, however, been impossible to use the better known popular names. For example, the well-known Tri-coloured Nun and Black-headed Nun have, along with several other forms, been merged into the species called here the Chestnut Mannikin. Also, the White-headed Nun and the Yellow-rumped Mannikin have been put together with several other forms as the Pale-headed Mannikin. The Rufous-backed Mannikin and the Blue-billed Mannikin are one with the Black-breasted Mannikin. Finally, the Indian Silverbill and the African Silverbill have been

merged simply as the Silverbill. The alterations in the generic names produce little confusion because the specific names are nearly always the same as in the earlier and better-known classifications. One awkward case is that of the Zebra Finch, which is still known throughout the avicultural world as *Taeniopygia castanotis* and here has had both its generic and its specific name altered.

It is not worthwhile to give in full here the earlier systems which Delacour has so drastically modified. To revive and discuss all the earlier latin names employed by older workers would only be confusing. But two other systems must be mentioned briefly. The first is that of Butler (1899). In a standard work on the aviculture of exotic finches, this author groups the estrildines under the same three headings as Delacour (i.e. waxbills, grassfinches and mannikins). His groupings differ strikingly in some respects from the later arrangement and the differences are therefore listed below. In order to simplify the situation, only the popular names are given, and where Butler has used one which is now out of date I have altered it appropriately :

Butler's arrangement

A. Waxbills.
Crimson Finch.
Painted Finch.
Fire-tailed Finch.
(Plus other Waxbills as in Delacour.)

B. Grassfinches.
Cutthroat Finch.
Silverbill.
(Plus other Grassfinches as in Delacour.)

C. Mannikins.
(As in Delacour.)

The other system concerns only the Australian species, but provides a valuable alternative way of grouping the members of the Grassfinch tribe. It has been worked out by the naturalist Mr. William Gordon (personal communication), who has been studying these birds in the Australian bush over a period of thirty years and who has bred all but two of the Australian species in captivity. He divides them into four groups as follows :

Gordon's arrangement

1. Fire-tailed Finches
Fire-tail Finch.
Red-eared Fire-tail Finch.
Red-browed Finch.
Diamond Sparrow.
Crimson Finch.
Star Finch.
Cherry Finch.
Painted Finch.

2. Grassfinches
Zebra Finch.
Bicheno Finch.
Parson Finch.
Masked Grassfinch.
Long-tailed Grassfinch.

3. **Munias**
   - Chestnut-breasted Mannikin.
   - Pale-headed Mannikin.
   - Pectoral Finch.
4. **Gouldian Finch.**

Here, as before, I have standardised the popular names.

With these three taxonomic arrangements as a starting point, it is now possible to survey critically the geographical, morphological and ethological data and to ascertain how and where any improvements can be made in the classification of the group. As already mentioned, the present investigation has been largely ethological, but a rapid glance at the geographical distribution and morphological variations of the estrildines nevertheless forms a valuable introduction to the behaviour material.

GEOGRAPHICAL DISTRIBUTION

The estrildines are an exclusively Old World group. Remarkably convergent ecological counterparts are to be found in the New World, in South America ; namely, the grasskeets (e.g. *Tiaris canora*, the Cuban Finch).

The Old World range of these birds may be roughly classified into three main areas : Africa, Asia, and Australia. The first and third of these are geographically precise, but the second is rather vague. It will be used here to cover everywhere in between Africa and Australia ; everywhere, that is, from Arabia, through India, down the archipelago to New Guinea and a few small islands beyond. If, having made this crude spatial distinction, the frequencies of the species from the three tribes are scored against the three regions, the following figures emerge (using Delacour's system) :

	African	Asiatic	Australian
Waxbills	**48**	2	1
Grassfinches	0	12	**14**
Mannikins	8	**26**	3

It is obvious from these figures that, geographically speaking, it is the mannikins that link the waxbills and the grassfinches, which contrasts with Delacour's suggestion that the grassfinches form a link between the waxbills and the mannikins. The ancestral home of the Ploceidae in general seems to be in Africa, and it is not unreasonable to suggest that the ancestral estrildines set out, so to speak, from Africa as a kind of primitive mannikin, leaving behind waxbills, scattering new mannikins as they went, and finally ending up in Australia with an outburst of grassfinches. This would, of course, necessitate some rather impressive convergences on the part of waxbills and grassfinches, but nothing more remarkable than many which have taken place between Old World and New World groups.

An alternative suggestion would be that certain primitive waxbills made the Asiatic trip to Australia to form the grassfinch group and that the mannikins were later specialisations which cropped up all along the range. Finally, a third and more complicated suggestion is that both waxbills and mannikins made the trek to Australia, where they both evolved new forms which have now been

wrongly lumped together as grassfinches. A detailed examination of the morphological and ethological data should help to make one of these three suggestions more plausible, or perhaps even to provide a fourth.

It is worthwhile to look for a moment at the geographically atypical members of the three tribes. Firstly, the non-African waxbills. These are the Red Avadavat (*Estrilda formosa*) and the Red-browed Finch, or so-called Sydney Waxbill (*Estrilda temporalis*). The range of the Red Avadavat is extensive, stretching from India and Ceylon, down through southern China and Siam to Java and even as far as Timor. In other words, it almost joins the African waxbills and the Australian grassfinches, and could be the remnant of an ancestoral waxbill movement to Australia. However, there are few obvious specific links with it in either Africa or Australia and it is aberrant in a number of ways, especially in having an eclipse plumage. (It is the only one of the 108 species to have this.) The Green Avadavat is restricted entirely to central India, and does not appear to provide any particularly valuable evolutionary clues.

The Red-browed Finch is taxonomically perhaps the most interesting of all the estrildines. It inhabits the extreme east of Australia. It has been called a waxbill (the Sydney Waxbill) by Butler and by Delacour, and yet has been placed without comment amongst other Australian grassfinches by Cayley (1932) and by Gordon. Geographically speaking it should be a grassfinch. As we shall see later, if it is to be considered as a waxbill, then a number of other Australian species should also be placed with the waxbills. Together these would represent a special waxbill invasion of Australia, distinct from the mannikin invasion. This is, incidentally, rather suggested by Butler's classification.

Next, there are eleven species of grassfinch which occur in the Asiatic region. Of these eleven, nine are the parrot finches. This whole group occurs outside Australia, and only one (*Erythrura trichroa*, the Blue-faced Parrot Finch) is found in Australia at all. However, the other parrot finches, although outside, are typically only just outside. Two species reach as far away as the Malay Peninsula, but most are found on the islands near to the north Australian coast.

Of the typical grassfinches, only three species are found outside Australia. One of these, the little-known Crimson-bellied Mountain Finch, inhabits only New Guinea, but the other two, the Crimson Finch and the Zebra Finch, are primarily Australian species that have gone just outside the area. The Crimson Finch is found over N. Australia and also S. New Guinea, but the Zebra Finch covers the whole of Australia and also occupies Timor and Flores.

On the basis of geographical distribution, then, one might be tempted to separate the grassfinches proper from the parrot finches. Plumage colour and markings would bear this out and Delacour gives no good positive reason for lumping these two types together in the same tribe, except that they have spotted rather than lined nestling palates. As will be shown below, this particular character cannot be used in this way, since the nestling palates of a number of the typical grassfinches are lined and not spotted. However, until some ethological data are obtained for the parrot finches, little more can be said on this subject.

Of the eleven mannikins which occur outside the Asiatic region, the three Australian ones are particularly interesting. They are the Pale-headed Mannikin, the Chestnut-breasted Mannikin and the Pectoral Finch. The first of these has the most typical mannikin appearance of the three and is also the one with the range that extends farthest into Asia. (As far as the Malay Peninsula.) The Pectoral Finch has the most unusual appearance for a mannikin and is confined entirely to N. Australia, while the Chestnut-breasted Mannikin is intermediate both in appearance and in distribution, occurring both in N. Australia and New Guinea.

The eight African mannikins, on the other hand, are a heterogeneous collection. There are the extremely distinctive Cutthroat and Red-headed Finches, which roughly cover the north and south of Africa respectively. The widespread Magpie, Black-breasted and Bronze Mannikins form another distinct little group, as do the Gray-headed and Common Silverbills. The latter is interesting as it forms a link with the Asiatic species, being the only estrildine which occurs both in Africa and Asia. Its range extends from central and northern Africa, through Arabia and Persia, to India and Ceylon. Finally there is the little-known and rather peculiar Bib Finch on Madagascar.

MORPHOLOGY

It is convenient, when discussing the comparative morphology of these birds, to consider mechanical and signal structures separately. Since this paper is concerned primarily with the comparative ethology of the group, emphasis will be given to the second category. There is, in any case, little to say about the first. The birds are almost all adapted to eating small grass-seeds and there is little variation in body proportions. Some species have turned to slightly larger or slightly smaller seeds, with an accompanying alteration in beak size (see Morris, 1955 e). The typical Asiatic mannikins, for example, often have massive beaks when compared with the waxbills or grassfinches.

Most species take their food while clinging to the grasses, but some prefer to feed from the ground. In a few of the latter cases, such as the Painted Finch, the birds have become specially adapted to ground living, with accompanying structural modifications. Most noticeable variant here is the toe-length. Mannikins are the best " clingers " and their toes have to be clipped repeatedly when they are kept in captivity to prevent them from becoming caught in the wire netting. They appear to be equally at home whether sitting upright, hanging downards, or clinging to a vertical. It is interesting to note that, with longer toes, there is a more upright carriage of the body. Presumably, shorter toes and a more horizontal deportment go together as adaptations to ground living in these birds.

Apart from the variations mentioned above, there is little of taxonomic value, as far as it is known at present, to be found amongst the slight mechanical-structural variations which exist in the group. Even the ones mentioned here are dubiously non-conservative and are really only helpful at the lowest levels. Indeed, one cannot help wondering why there should be so many

species of estrildines, when it seems as if a fraction of the number would have been just as efficient ecologically. Clearly, a detailed comparative field study is required to solve this particular problem.

There are, however, some valuable taxonomic clues to be gained from a study of the signal morphology of the estrildines. By this, I refer, of course, to the elaborate plumage markings and colours, to the beak and leg colours, and to the nestling mouth markings.

In general, the waxbills and grassfinches are more brightly adorned than the mannikins. This applies not only to plumage colours, but also to leg and beak colours. The mannikins nearly all present a combination of white, grey, brown and black, or one, or some, of these. The other groups exhibit an exotic range of reds, yellows, blues, greens and even mauves and violets. There are a few exceptions to this rule, one or two of the mannikins having bright patches and one or two grassfinches and waxbills being sombre in appearance. The mannikin exceptions are the Cutthroat Finch, in which the male possesses a bright red throat patch, the Java Sparrow, in which both sexes have a pink beak, and the Bib Finch, which has a black and red beak and pink legs. Comparatively dull coloured grassfinches include the Parson Finch and the Bicheno Finch, which are entirely black, buff, white and grey, and the Long-tailed Grassfinch, which is similar but which has a brightly coloured beak. (Waxbills not dealt with here.)

Details of the plumage of each species will not be given here, but a few examples, of the way in which plumage differences and similarities can be useful aids to understanding relationships in the present group, may be mentioned. Firstly, there are interesting cases of what appear to be extraordinary convergencies. For example, the Red-browed Finch in Australia and the Red-eared Waxbill in Africa both have plain greyish bodies, with no special markings: both have bright red beaks and both have bright red eye-streaks. This superficial resemblance, however, does not stand closer scrutiny, when it can be seen that the eyestreak of the Australian species passes more over than through the eye, whereas that of the African species passes straight through the middle. Also, the red of the beaks and the body-grey is different in the two cases. The relationship between the African Fire-Finch and the Australian Crimson Finch is similar. Both have crimson plumage which is brighter in the male; both have red beaks and distinctive yellowish eye-rings, and both have tiny white spots on their flank feathers. Nevertheless, a close examination of the plumage of these birds also brings one to the conclusion that this is a case of convergence; for none of the details tally perfectly, one giving the impression of being a bad imitation of the other.

Contrasting with this, there are series of species in which there are many different patches on certain parts of the body but one or two conservative patches which remain constant through the series and which are, upon close scutiny, clearly of common origin. Take, for example, the characteristic black and white rump-to-vent markings of the Masked, Long-tail, and Parson Finches, or the dark brown face masks of the Pectoral and Chestnut-breasted Finches. Close examination reveals these to be more than just similar superficially. They also bear striking resemblances in indefinable subleties of quality.

Distinguishing between resemblances which are the result of convergence and those which are not is difficult to discuss in words (Lorenz (1953, p. 1) has described this difficulty at some length). It is not easy to demonstrate even with skins. One simply has to spend a great deal of time making detailed observations of the living birds at close quarters in captivity. Only then, for example, does one begin to notice that the red eye-brow of the Red-browed Finch is more genuinely related to the red face mask of the Crimson Finch, than it is to the superficially more similar eye-streak of the Red-eared Waxbill. Observations of this kind will not be set out in detail here, but their significance will automatically be taken into account when taxonomic relationships are being considered later in the paper.

One final aspect of the morphology of the estrildines must now be considered, namely the important mouth-markings of the nestlings. Briefly, these markings are black spots or lines on the palate, tongue, or elsewhere inside the mouth. In some species, the typical white gapes are elaborated by colours, warts, or lobes, but these will not be discussed further here. There are three basic types of palatal marking, as illustrated in Morris, 1955 c. One of these three is limited to the Cutthroat Finch and consists of large blotches. These form a pattern similar to that made by the spots of the second type. However, if the blotches are joined up in a certain way, they are similar in pattern to the third, namely lined-palate, type. In other words, although it can be said that the Cutthroat Finch is aberrant as regards its nestling palate markings, it cannot be said whether it is more similar basically to the spotted or lined types. According to Delacour, all waxbills and grassfinches have spots (one to seven in number), whereas all mannikins have semi-circular lines. He considers these markings to be of great taxonomic value at the tribal level. However, the situation is not as simple as this. At least five species of grassfinches have lines and not spots. Three of these are the very closely related Parson, Long-tail, and Masked Grassfinches. Delacour admits that these have "short lines" but does not consider them to be typical lined-palate types. Both Parson and Long-tail Grassfinches were bred during the present investigation and, although detailed study was impossible, because it was necessary to interfere with the nestlings as little as possible, it was nevertheless apparent that there is nothing very unusual about their palate-lines. In other words, if tribal affiliation is determined exclusively by this nestling mouth-marking character, then these three Australian species are good mannikins. Since Delacour states that "As long as the mouth pattern of every species has not been finally recorded, some doubt will remain as to the position of a few species", it is clear that he does in fact think of this single character as being tribally all-important. He should, therefore, take these three species out of the grassfinches and place them with the mannikins. He has placed the Pectoral Finch with the mannikins because of an avicultural report that its nestlings have lines and not spots and should not therefore be inconsistent without explaining the inconsistency.

The Star Finch was also bred during the present study and this too produced nestlings with lined and not spotted palates. This species has not had this character recorded before and on other characters was placed with the grass-

finches by Delacour. On his system, this too should now become a mannikin. The same applies to the Cherry Finch. Of this species, Delacour states that it resembles the Silverbill (it was placed in the same genus in older systems), but that he is " convinced that there is no real close relationship between them. When we know the palate markings of this species, we shall be able to finally decided on this point ". It is now known that the Cherry Finch also has lined and not spotted palate markings in the nestling (Poulsen, personal communication, concerning observation by Enehjelm). Presumably, therefore, in this case Delacour would abandon his conviction about the affinities of this species, because of one character being out of place. Although I have not been able to study this particular species myself, I would prefer to trust Delacour's general conviction, rather than follow his devotion to a single character.

One only has to look at the structure and behaviour of these " awkward " species for it to be quite clear that it would require a great deal more than one small black line to tie them to the mannikin group. The fact that they possess these lines can only mean one of two things. Firstly it may mean that the palate markings are not the conservative characters they were thought to be and that they are the result of some special adaptations to, say, feeding habits. As soon as one species takes up a certain type of food niche, it may be an advantage for it to have the roof of the mouth (in the adult) grooved in a special way. The black spots and lines of the nestlings, which fade with maturity, are typically arranged around raised white ridges. These ridges are simpler in the lined species than in the spotted ones. In the latter, fingers extend from the main curved ridge and the spots occur in between these. It is conceivable that feeding habits are related to ridge-type and that ridge-type determines palate markings. This would mean that convergences would be expected to occur. So far it has not been possible to test this hypothesis. A field study of many different species, their food, and their palate markings, would give the answer.

Secondly, the existence of five " lined " grassfinches may be of great evolutionary significance and, if the first suggestion above is not the case, these five species may be all-important intermediates between the typical mannikins and the typical grassfinches. It would however be ridiculous to place them with the mannikins. On the other hand, it makes the grassfinch group more heterogenous than ever and once again raises the problem of whether this is really one or two natural groups of birds. Are these five species comparatively unrelated to the " spotted " grassfinches, or not ? It is possible that from the ancestors of the " lined " grassfinches came the " spotted " ones or, alternatively, that the " spotted " types represent a separate waxbill invasion of Australia. As already pointed out this is perhaps the most interesting estrildine evolutionary problem.

If we look at the various characteristics of the " spotted " Zebra Finch, Gouldian Finch and Bicheno Finch, we find that these species in many ways appear to be genuinely related to the " lined " grassfinch species and it seems likely that they have close affinities and have nothing to do with a Waxbill invasion. On the other hand, the " spotted " Red-browed Finch, Painted Finch and Crimson Finch, appear to be closer to the waxbills in many ways,

and may well represent a separate invasion from a waxbill ancestor. The existence of one species, namely the Diamond Sparrow, makes this unlikely. It is completely intermediate between the waxbill-like group and the others. It is impossible to say whether it belongs to one or the other and therefore makes it seem slightly more likely that the whole of the Australian estrildine group is derived from ancestoral mannikin stock, which swung round to a very striking convergence with the African waxbills. This is still tentative as a conclusion and it must be emphasized that a further study of these particular species, mentioned above, would be most rewarding.

These morphological considerations and the geographical ones discussed earlier must be kept in mind as a background to the ethological findings given on the following pages. They render the immediate assessment of the significance of a particular behaviour similarity, or difference, an easier task.

ETHOLOGY

In many ways, the estrildines are ethologically extremely homogeneous. They form a very natural and distinct subfamily of the Ploceidae, from the point of view of their behaviour. Certain actions appear in all species of estrildines so far studied, but appear in none of the other Ploceidae groups. The tail-quivering soliciting of the sexually motivated female is such a pattern. In most other Ploceidae, the female shows sexual willingness by wing-quivering. However, we are primarily interested here in relationships within the Estrildinae and for these we have to turn almost exclusively to the sexual behaviour of the males. But first, there exist a few points of taxonomic interest in the agonistic and nest-building patterns and these will be briefly outlined.

Agonistic behaviour

The fighting behaviour of estrildines is comparatively simple. The report given earlier for the Zebra Finch (Morris, 1954 a) applies to almost all species. Birds which are well-matched, beak-fence by standing in a sleeked vertical posture and stabbing at one another's beaks. The mandibles are usually closed and little damage appears to be done. If one bird is much weaker than the other, the dominant aggressor attacks in a frontal-horizontal posture, again with feathers sleeked, and either stabs or plucks.

During fighting many species utter tsit-tsit-tsit cries. Others fight silently. Song is not typically employed in agonistic situations, being basically a sexual device with estrildines.

Motivationally, the above can be summarised as follows. When the tendency to flee and to attack a rival are approximately in balance, the bird assumes a vertical posture and beak-fences. When the tendency to attack is much stronger than the tendency to flee, it assumes a frontal horizontal posture and charges the rival. Plucking, as opposed to stabbing, in the latter case, appears to be the result of an even more intense aggressive motivation.

This, then, is the basic story for almost all species studied, but it remains to mention the few exceptions to these rules, which are perhaps of some taxonomic significance.

One exception concerns the sleeking of the feathers. Certain species erect the crest when attacking or threatening. This is not done in an all-out fearless charge, but usually in an aggressive situation where there is a little fear present. In the photograph in Fig. 1 in Morris 1955 d, there is just discernable the erected crest of the threatening male Crimson Finch. In the full threat display of this species, the very long tail is raised and slightly fanned, and the crest fully erected. This is done when the body is in the frontal horizontal charge posture, but at moments when the bird is actually hesitating about going in to the attack. Certain other Australian estrildines, notably the Parson Finch, Long-tailed Grassfinch and occasionally the Zebra Finch, also erect their crests in agonistic situations. So far, however, it has not been possible to ascertain with certainty, with these other species, exactly what motivational situation is correlated with this response. Crest erection in these species is at the present stage rather unpredictable and is not apparently used in the same way as in the Crimson Finch.

A general fluffing of all the body feathers has been observed as an appeasement device in several species and is probably of widespread occurrence throughout the group. Juvenile food-begging has also been observed as an appeasement gesture by submissive individuals, but only in two species. One was the Zebra Finch and, as already reported in a previous paper (Morris, 1954 a), a badly persecuted female achieved momentary respite from her aggressive mate by begging to him. When being very badly beaten, she crouched and twisted her neck round in the typical estrildine nestling manner. The other species was the Java Sparrow. Here the juvenile response was given more freely and frequently. In a social encounter, either intra-, or inter-specific, a Java Sparrow which was not prepared to become involved in a fight when challenged, and yet was not prepared to flee, or could not flee, gave the high intensity " neck-waving " response. This is a very characteristic response of begging nestlings. They either twist their necks round and then wave their heads from side to side slowly and rhythmically, or they stretch their necks forwards and upwards (at an angle of about 30 degrees from the horizontal) and then proceed to wave the extended neck from side to side. The beak, of course, is wide open during this ceremony and in the adult Java Sparrows this is also the case. (It is interesting to note that Brooksbank, 1949, p. 45, reports that newly-hatched Chestnut-breasted Finches " have a short bulbous tongue which they roll to and fro with a rhythmic swinging motion. . . ". One would predict that extreme submission in this species would involve this special response.)

It is perhaps worthwhile to mention at this stage that there does not appear to be any courtship feeding amongst the estrildines, or, at least, no elaborate or common ceremony of this kind, during the pair-formation and maintenance phases. Adult food-begging is only seen in submissive agonistic situations.

In a recent monograph on the Bronze Mannikin (Morris, 1957 b), the specialized fighting postures of this bird were discussed in full. Briefly, this bird shows the aggressive frontal-horizontal charge, but does not possess the vertical posture for beak-fencing. It beak-fences extremely savagely, however,

adopting a latero-horizontal posture during bouts. The bodies of the two contestants are parallel to one another, and the heads twisted round to face the opponent. In addition to this, they exhibit a one-wing-up display whilst beak-fencing. This involves the wing farthest from the rival, which is held vertically during the stabbing and which is brought down vigorously as a means to establish balance if the bird feels itself being thrust backwards. The Black-breasted Mannikin is a close relative of the Bronze Mannikin and shares its fighting techniques. It would be valuable to know if the larger, but similar, Magpie Mannikin also uses these fighting techniques. If it does, then there are probably sufficient similarities between these three birds, and sufficient differences between them and other Mannikins, to warrant re-placing them into a separate genus (*Spermestes*).

The Long-tailed Grassfinch also beak-fences in what is practically a horizontal posture. The head is drawn back more than in a fearless charge, but the body remains horizontal (see Pl. 1, figs. 1 and 2). There is no special one-wing-up display in this species, however, although the far wing is employed to establish balance occasionally (see Pl. 1, fig. 2). Its use as a balancer is, interestingly, less obvious and spectacular than in the Bronze Mannikin or the Black-breasted and, correlated with this is the fact that the two mannikins possess bright markings on their wings, but the Long-tailed Grassfinch does not. The horizontality of the beak-fencing of the Long-tailed Grassfinch differs too in another way from that of the mannikins. The latter often assume a very vertical body posture, when alert or alarmed, but the grassfinch is an almost permanently horizontal bird. It holds its body well down out of the vertical during almost all its activities and the horizontality of its fencing appears to be simply a by-product of the general deportment of the species. In the case of the mannikins, on the other hand, it must be a more specialised independent development.

Nesting behaviour

As far as is known, no estrildine species is a true weaver when building its nest. The structure is a clumsily built spheroid with a side entrance. The entrance tunnel is never great in length, as in many of the true weaver species. Three basic movements are used in building the nest, apart from the obvious ones of collecting grass and placing it on the nest site. One is "testing", in which the bird holds the grass or straw between its mandibles and then opens and shuts the latter with extreme rapidity. This action of the mandibles has been called mandibulation and is extremely interesting in its ritualised signal role in sexual behaviour. All species appear to exhibit this action.

Next, there is "looping", which is an elaboration of "testing". Here, the grass is placed under one foot and held thus while the bird mandibulates it. It may then be transferred by the beak from one foot to the other, or its position shifted, to test a new length (elasticity is an important attribute of nest material; brittle grasses are inefficient and the testing is probably concerned with checking this quality), or it may be looped round several times under the foot. The important point about looping is not its use as a ritual, but its occurrence in only certain species. Many estrildines show it, but a

number of others do not. It is, of course, difficult to say that a species does *not* do a particular thing : it may simply be that the observer has not yet been lucky with the species. It is dangerous, therefore, to divide the species studied into those which do hold down nest material with their feet and those which do not. Once a species has been seen to perform this action it is easy, but a species which has never been observed to do so has to be very well-known indeed before any negative statement can be made about it. (This applies also to all the other characters dealt with in this and other studies of a comparative nature, where a behaviour character is simply present or absent.)

The Zebra Finch is now known well enough to be considered with certainty as a species without foot-holding during nesting. There are several other species which also appear to belong to this category, but they will not be named until more observations have been carried out. On the other hand, species as different as the Star Finch, Red-browed Finch, Spice Finch and Bronze Mannikin have all been observed to hold down nest material with their feet. (There is a possibility that toe-length is involved here ; holders seem to be long-toed and non-holders short-toed.)

The third important nesting action is " neck-stretching " or " scooping ". This is performed inside the nest cup and helps to form the sides and roof of the domed structure. The neck is stretched in a characteristic way, pushing the nest material away or up and thus scooping out a discrete nest cavity. This action appears to exist in all species and is most important in its role as a ritualized sexual signal. It has become modified in different ways in different species and now exists in a whole series of ritual forms. These will be discussed in the next sections.

Sexual behaviour

As the comparative data available for this section are rather complex, they will first be dealt with species by species before an attempt is made to summarise their taxonomic significances.

It is impossible in this paper to subdivide the sexual patterns into pairing and pre-copulatory activities, because a particular action which appears in the pair-forming stages in one species is associated with the pre-copulatory patterns of another species. A further confusion exists because of the intimate connection between reproductive nest-building and pairing in certain species (see Morris, 1957 b). Nest ceremonies and pairing ceremonies appear to be one and the same and nesting actions have thus worked their way into the sexual repertoire and even into the pre-copulatory patterns in some cases. This is probably the result of the fact that the social nesting each night, of the non-reproductive group, fragments into private reproductive nesting simultaneously with the forming of the pairs. As the pair forms and the mated birds develop aggression towards their earlier sleeping companions, they also develop a stronger nesting urge, which leads to the more elaborate domed breeding nest. (The social roosting nest is little more than a crude platform in most cases.) Higher intensity nest-building is therefore irrevocably linked with the vital phases of pair-formation and the nesting actions have thus taken on a sexual significance and act as social signals. Almost all the species described below

will be found to have some kind of nesting act built in to their sexual signal codes in some way or other.

Although, as stated above, these facts make it difficult to discuss first the pairing behaviour of all the species and then the pre-copulatory behaviour of all the species, it is nevertheless possible to make this sexual subdivision in the case of certain better known-species and this will be done in the particular cases concerned. Those species already dealt with in earlier papers will be summarised very briefly here for the sake of uniformity. With these few preliminary remarks it is now possible to deal with the sexual patterns species by species, employing the order used by Delacour in his revision of the group, with one modification. The latter concerns the Red-browed Finch which, as a waxbill, should be placed first. Since we are not considering waxbills in this paper, this species really should not be dealt with at all, but owing to the dubious nature of its present taxonomic position, its patterns will be described here, after the grassfinches and mannikins have been dealt with. Although it should already be clear that I do not agree with all of them, I shall use here Delacour's generic and subgeneric divisions, so that behaviour similarities and differences can be seen against the background of his taxonomic arrangement, which, despite one or two difficulties, is still the best arrangement of the whole group so far produced.

A. Grassfinches :

Genus *Zonaeginthus*

Subgenus *Zonaeginthus*

1. *Z. pictus* (Painted Finch). Central and N.W. Australia

Webber (1946) states that when the male of this species courts he does so with " head held up, beak 60 degrees from horizontal " ; also that " the head is moved smartly from side to side " and that there is no " bobbing up and down on the perch . . . a popular method with other Australian Finches ". However, in an appendix to the paper, Webber mentions that he finally did observe a male which " held a grass stalk in his bill, crouched over the perch, bobbed up and down and more or less performed the Diamond Sparrow display ". (For description of latter see below.) It is almost certain that this last account gives the correct description of the full display of the Painted Finch. It seems very likely that Webber was describing the non-courtship singing as part of the courtship, until he finally saw the true courtship dance, as he reported it in his appendix. (Although it has been dealt with fully elsewhere, it should perhaps be explained here that males may sing without courting but rarely court without singing. The non-courtship singing is either given by solitary birds, or, if others are present, the male does not orientate to them in any way. In most species, the posturing accompanying the two types of singing differs. Unorientated singing is typically accompanied by a lower intensity version of the courtship singing posture. The various characteristics are seen in both, but usually all are exaggerated in the courtship cases. In some species, there is little or no such difference, but in most it is obvious enough.)

Gordon (personal communication) stresses that this species is a " ground-lover " and reports that this influences the form of its courtship slightly. He says that " The males display without a straw. They strut upon the ground, picking up and dropping bits of earth, straw, etc. Then, head back, bill up, body erect, they sing, while they shuffle in jerky hops to female. Males dominant sex. The " chase-flight " and female behaviour are similar to the other Firetail species ".

There appear to be some contradictions between Webber's and Gordon's observations, but this is undoubtedly the result of the fact that this species, which certainly is more of a ground dweller than most estrildines, courts both on the ground and also when perched. The different position of the courtship would undoubtedly influence its form, and this appears to be the explanation here, Webber having watched perched courting and Gordon courting on the ground. It is most interesting that the carrying of the straw or grass in the beak during perched courtship is changed to picking up and dropping material when on the ground, and shows the extent to which the external environment can influence the details of the courtship ceremony.

Both authors stress that the beak is tilted upwards during singing and this is a point of great comparative importance. I can confirm that it occurs, from personal observations of the few Painted Finches I was able to obtain. The following are observation notes made on the behaviour of these birds :

" Solitary song is performed without special feather raising, but with a distinct head pivoting. The beak is pointed upwards and is thus reminiscent of the Red Avadavat. The beak is not opened appreciably during song. The song phrase is repeated typically two or three times in each song-bout. Like almost all Estrildine songs, it is difficult to represent verbally but is structurally rather like : che che che-che-che-che-che werreeeeee - oooeeeeee. Sometimes, the last two phrases are the same as one another, when they sound more like : cheeurr cheeurr. This alternative never occurs in the first phrase of a song, usually only in the second phrase of a two-phrase song. In other words, it looks as though, in this species, the song is already becoming something more complex than just the simple repetition of a single phrase ".

It was noted at the time that the song posture including the pivoting of the up-turned beak, was similar to that of the Red Avadavat, and also that certain aspects of the plumage colouring and marking were similar. The distribution of the Avadavat (extending down to Timor, off the N.W. coast of Australia) and the rather unusual distribution of the Painted Finch (from the N.W. coast of Australia in to central Australia) strongly suggest the possibility that here we are dealing with a separate waxbill invasion of Australia. This will be discussed again later.

Only very brief courtship observations were possible with the Painted Finches used in the present study and the more elaborate display seen by Webber was not recorded. The following details were noted :

" Female presented to male. He approaches her and she responds by twisting her tail round towards him. He faces her and his first action is to toss his head back for a second. Then he starts singing to her in a rather vertical posture, with legs stretched somewhat, with the head thrown back

and with very rapid head pivots (latter being most noticeable feature). No striking raising of feathers. Then he mounts her unsuccessfully. . . "

In subsequent courtships, the male was seen to perform displacement beak-wiping both before and during display bouts and both male and female preened afterwards. On several occasions, the courtship broke down into beak-fencing in which the male's beak was open and pushed over the closed beak of the female. Both male and female showed the tail-twisting response at various times during courtship bouts : in both sexes the tail is twisted round towards the partner. Finally, it was noticed that the courted female's posture included a tilting up of the beak. Both this tilting and the tilting up of the courting male's beak were sustained actions. The head was tilted back and held there while the courtship proceeded, in contrast with the male's initial, momentary, head-tossing mentioned above. This quick head tossing is seen in this species during beak-fencing when it alternates with stabbing forwards and is performed by a silent male. As soon as he begins to sing, the male's head is tossed back and held there throughout the singing.

Fragmentary as these notes are for this species, they give a number of important clues. Most significant of these is the raising, rather than lowering, of the beak in social encounters. This is, according to Delacour, a typical waxbill characteristic. The Red-browed Finch also possesses this movement and this is one of the main reasons for this bird being included with the waxbill group, despite its geographical position. The observations recorded here for the Painted Finch—a supposed grassfinch—therefore create an inconsistency in the present taxonomic system.

2. *Z. bellus* (Firetail Finch). E. Australia and Tasmania

Little is known about this species which, for some unspecified reason, is extremely difficult to keep in captivity. Butler (1899) records that the " love-dance is like that of the Diamond Finch " (the Diamond Sparrow, see below).

3. *Z. guttatus* (Diamond Sparrow). E. Australia

This rather heavily built species has a mournful low-pitched call-note reminiscent of the *Poephila acuticauda, cincta, personata* group. Its display has been recorded by several authors, as follows :

Butler (1899) reports that the male, in his courtship " stretches his neck upwards to an extravagant height, draws in the breast and expands the chest and abdomen, stands very upright and with depressed head, a long grass bent in his beak, then bobs up and down on his perch, to the accompaniment of his queer song ". Cayley (1932) says that the male courtship is " A measured curtseying, head directed downards, so that the beak almost rests upon the breast " ; also that " he stretches his neck, holding a long straw in his bill, stands right up on his legs and hops up and down at the side of his mate like an automaton, approaching along the perch as she retires ". Brooksbank (1949) describes the performance as follows : " Having procured the longest bit of grass he can find, the cock holds it at one end in his beak and puffs his feathers

out to such an extent that he not only appears to have doubled his size, but looks almost spherical in shape. He literally bounces about like a ball, at the same time buzzing like a bumble bee . . . "

These reports tally fairly accurately and together give a clear picture of the display. The angle of the beak is again a feature of the display which catches the attention of the observers and it is interesting that it is as different as it could be from the last species.

Genus *Poephila*

Subgenus *Neochmia*

4. *P. phaeton* (Crimson Finch). N. Australia and S. New Guinea

Butler (1899) says of the display : " song a comical humming with the head raised high, a zealously moved beak and fan-shaped, outspread tail, turning in a dignified manner from one side to the other and then breaking off from the marvellous, noiseless, love-dance suddenly with a loud whistle ". From this report, the basic dance movement appears to be of a lateral pivoting nature, but Cayley (1932) gives a slightly different picture : " The long tail-feathers are spread out like a fan, the body carried very erect, and the head is moved from side to side in a most dignified manner . . . sometimes, if on a thin twig, he bobs up and down and sways the outspread tail-feathers ". Harman (1953) confirms certain of the above features when he states that " The tail is spread out fanwise and the body held very erect. While humming a curious note, the males move their heads slowly from side to side in a most dignified manner ".

From these three reports it appears that the fanning of the tail, the erection of the body and the pivoting of the head and/or body are the salient features. A vertical dance movement is also suggested by Cayley's comments and, as will become clear below, the possession of both dance movements, either combined or separately, is a feature of a number of species' displays. The fact that the tail is fanned by very aggressive male Crimson Finches during attacks suggests that there may be a considerable aggressive element in the courtship of the male of this species.

It was only possible to observe the behaviour of a single pair of this species in any detail during the present study. The male concerned was provided with a female, with the following immediate results : " Male threatens with tail-up-and-fanned. Does not actually attack. Male beak wipes. Sings to female ; song phrase : chu chu chu che-chee chooo. Posture is horizontal, not vertical. Both male and female in horizontal posture, parallel to one another, with heads and tails strongly twisted towards the partner. No feather raising except for face mask, crown and nape, as in threat display. Legs rather stretched. Flank feathers outside the wings, but not exaggeratedly. The male display begins with rapid ritualised beak-wipe bows—never touching the branch, but obvious in their derivation. These are rapidly and rhythmically repeated—each appears to be a separate wiping, but each abbreviated. When female comes near the male, she too raises her face mask and, as she approaches close, he changes to an upright posture. After the first phase of courtship

breaks off, the male flies about and, for the first time, it is noticeable that he tosses his head back each time on alighting ".

In later courtship bouts it was noticed that the male made slight pivoting inverted-curtsey movements while singing to the female. The courtship sometimes broke down into an attack by the male. The head of the male when singing was not seen to move at all ; nor was the beak. The female was observed to tail-quiver as a sexual invitation, but the male did not respond by mounting.

There are apparent contradictions here between the reports from the literature and these personal observations. There is however, an explanation for this. In several species (e.g. Spice Finch, Moynihan & Hall, 1954), it has been found that an unduly aggressive male courtship involves a special horizontal posture called, by Moynihan & Hall, the " low twist ". This does not appear in a typical courtship, which may be quite vertical. It seems that in the present case, the male under observation was much more aggressive than those studied by the earlier authors. Its attacks on the female and the raising of the same feathers as in normal threat confirm this. The fanning of the tail in courtship and in threat, as reported by others, reveals that there is probably always an element of aggression present, but in my own male, the extra aggressiveness appears to have changed his posture from vertical to horizontal and eliminated head and beak movement. This idea is reinforced by the fact that the approach towards the male of the female changed his position to a vertical one. Her approach would be expected either to reduce his aggression or to directly arouse his sexual tendencies, or both, and would therefore be expected to produce the more sexual, vertical posture. Finally, both dance movements, vertical and horizontal, appear to be available to this species and it seems likely that they may, as in the Spice Finch, appear either separately or combined.

This species shows certain striking resemblances to the Painted Finch, as regards its behaviour. Both have a characteristic multiple call-note (che che che che che che) which is so similar that they were heard to answer one another from different aviaries. Other grassfinches and mannikins studied were found to have only a single call-note, although multiple call-notes were heard in certain African waxbills. The tossing-up quickly of the head was also shared by the Painted and Crimson Finch, but was not seen elsewhere in the grassfinch and mannikin groups. The red face masks of the two species, and certain other markings are also not dissimilar, although the general visual impression is superficially rather different.

Owing to the extremely savage nature of this species in captivity, it is a difficult bird to study, but clearly it is a most important species and demands much further study. (For photographs of its aggressive behaviour, see Morris, 1955 d).

5. *P. ruficauda* (Star Finch). N. and E. Australia

Cayley (1932) mentions the fact that the male " often carried a piece of grass in his beak during the mating display . . . " and he quotes the observations of a number of aviculturists, one (A. E. Clarke) as saying that " When

mating, I have noticed both the male and female with bits of grass in their bills, and they both bob up and down before each other ". However, another (J. S. Mackie) reports of a male of this species that " when mating he danced from side to side with his tail spread ".

From personal observations of this species, I can confirm the importance of straw carrying as a ceremonial, although, unlike Clarke, I have only seen it in the male. The carrying of straw as a ceremonial is accompanied by an elaborate bowing display which is presumably what Clarke refers to as " bobbing " up and down. The statement that a bird bobs up and down is unfortunately an extremely ambiguous description. There are so many subtly, but importantly, different ways in which it can move up and down. Each way appears to be derived from a basically different movement and the ceremonies should not therefore be compared too glibly. In the bowing of the straw-carrying male Star Finch, the movements are repeated and deliberate. The bird bows rhythmically keeping the beak horizontal both at the top and at the bottom of the bow. In this way, it differs distinctly from the bowing of most other courting estrildines. Usually the ceremonial bow is derived from displacement beak-wiping and then the beak points more and more downwards as the body is lowered in the bow. The Star Finch bow is almost certainly derived from a different source, namely the intention movements of taking-off for level flight. If observations are made of finches about to fly away from a branch horizontally, similar quick bowing actions can be seen. These have become more ponderous and dignified in the ceremonial bow of the Star Finch but are still quite recognisable. It seems as if the male is using as a sexual display that phase of nest-building where he would be repeatedly flying to the nest with material. He is therefore performing a fundamentally different (but superficially similar) display from the beak-wipe bowing of the other grass-finches and mannikins. The only other species of estrildine in which I have seen a similar bow is the Red Avadavat, where both male and female show the response, again with a grass or straw in the beak. This and certain other features mentioned below seem to relate the Star Finch to the waxbill-like grassfinch group, but there are difficulties here. For example, this is one of the five species of grassfinch which has the mannikin-like lined nestling palate. Like the Diamond Sparrow, this is an extremely awkward species, taxonomically speaking.

The solitary song posture of this species and its relationship to the resting posture are illustrated by the photographs in Pl. 1, figs. 3 and 4. It will be seen that the male does not erect his ventral feathers, but does raise his breast feathers and his face mask. This is practically the reverse of most estrildines. In nearly all the other species, the ventral feathers are erect and the breast feathers depressed. Only in the case of the Silverbill is there a song posture with sleeked ventral feathers as in the Star Finch. It is worth noting that the erected region is just that area which is brightly marked with white spots, the ventral region being unmarked.

The song is reminiscent of that of the Zebra Finch, but is of a higher pitch. The call notes and other squeaks uttered when beak-fencing are extremely high pitched. When the male starts a high intensity courtship display with

song, the solitary singing posture is exaggerated into a unique posture. The legs are stretched vertically so that, with the ventral sleeking, the male has its body raised as much as possible above the perch. The feather erections noted for the solitary song are now intensely exaggerated ; all the spotted regions (that is, the flanks and breast, and around the red face mask) are fully erected. The flank feathers stand out strongly from the body, with the wings tucked away inside them. The male is ridigidly horizontal and faces the female thus. Viewed from directly in front, or from directly behind, the flank feathers can be seen standing away from the body very distinctly. The female has a perfect view of all the spotted regions and, although it was not observed in the present case, it is obvious that a pivoting dance movement (as mentioned by Mackie) would show off the spots even more. Head pivoting was seen in the singing males, but not the full body pivot.

Tail-twisting towards the partner was seen in both sexes with rather a high frequency during sexual encounters.

Before proceeding to the next species, it is perhaps worthwhile to record in detail the most complete courtship sequence observed, because this reveals the sequential relationship between the straw-carrying-and-bowing display and the feather-erection-and-singing display :

" Male hunts for straw and selects longest one it can find. Then takes up lateral sleeked position across branch and starts to bow with straw in beak. Bows rather rapid (two a second) and less pompous and deep than the Red Avadavat bowing. He bows 11–12 times, interspersed with two or three advances towards the female. Then bowing stops, but male holds horizontal lateral posture. He continues to advance, nearer the female with straw in beak, but now he sings instead of bowing. The posture is intermediate between normal song courting posture and sleeked bowing posture. When he gets very near the female, he drops the straw and mounts her. She opens her cloaca, but does not quiver tail. He dismounts, but before doing so he mandibulates. He seemed to be mandibulating because for some reason he could not copulate ".

In other words, the straw-and-bowing ceremony is phase one of the male's courtship and, almost certainly, the singing in phase two, which supercedes the bowing, is accompanied by lateral dance movements at higher intensities. The peculiar horizontal, leg-stretched, courting posture of phase two is undoubtedly derived from the take-off for level flight is as the bowing. Electronic flash photographs of birds which are caught in the moment immediately before they leave the perch for level flight often look very similar posturally to the courting male Star Finch in phase two.

This bi-phasic male courtship makes an interesting comparison with that of the Spice Finch. Here, Moynihan & Hall (1954) describe how the male and female hop back and forth carrying straws until one lands near the other, when the male drops his straw and begins to sing to the female in the (phase two) courtship posture. In the Spice Finch, then, the ceremonial straw-bowing is absent and in its place hopping back and forth occurs. Also, the straw is dropped before singing starts and not after it as in the Star Finch. Correlated with this is the fact that the Star Finch sings with a closed beak and the Spice Finch opens and shuts its beak while singing.

It seems as if, in these species, the earlier stages of nesting are being incorporated into the courtship ceremonies, whereas in certain other species the later (scooping) stages are used.

6. *P. guttata* (Zebra Finch). Australia, Timor, and Flores.

Previous papers have dealt with this species in detail (see Morris, 1954 a, 1955 a, and 1956 b). Its behaviour will therefore only be briefly summarised here :

Male courtship consists of song with vertical posture, beak horizontal, ventral feathers fully fluffed, crown feathers flattened, nape erect, spotted flank feathers erect and held outside wings (see Pl. 1, fig. 4). Head pivots rhythmically in both solitary and pre-copulatory song display, but, in latter, whole body performs lateral pivoting as well. Beak does not open appreciably during singing. Legs fully bent ; birds ventral feathers rest on perch. Aggressive courter has body more out of vertical plane and pointing more towards female than non-aggressive courter. Tail-twisting towards female by courting male observed frequently, but never by female to male as in some other species. Male repeatedly bows to female during his pivoting advance towards her, but these bows are clearly derived from displacement beak-wiping movements and they often develop into full beak-wiping. Female also may beak-wipe occasionally whilst being courted.

The Zebra Finch was never observed to perform the vertical, inverted-curtsey, dance movement seen in so many other species, despite prolonged observations. A sentence from Cayley (1932) made it seem likely that the vertical movement might occur under certain circumstances, however : " Usually the singer carries his head erect, with the neck outstretched, and jerks its body up and down, or sways to and fro ; the latter movement is chiefly adopted by the male during the breeding season ". Since the Zebra Finches used in the original study (Morris, 1954 a) were all " domesticated " stock (probably bred for as long as thirty generations in captivity) a group of wild-caught Zebra Finches was sought and when obtained was set up in a colony along-side an equal number of " domesticated " birds. If the absence of the vertical dance movement was the result of using special stock, then this set of wild-domestic observations should have revealed it. However, apart from the fact that the wild Zebra Finches were smaller than the " domestic " ones, there was no discernable difference between their behaviour. This can only mean that, if the vertical dance movement is really ever given by this species, it must require special conditions for its performance which are not available in captivity. (In a number of other species, the vertical movement does, of course, occur quite readily in captivity and, in some, it occurs more readily than the horizontal pivoting movement.)

One behaviour pattern of the Zebra Finch, which was seen for the first time after the previous reports on this species had been completed, warrants special mention here, because it provides an important link between this species and the Long-tailed Grassfinch. Both these have a pairing ceremony of a somewhat unusual derivational nature. The pairing behaviour of the Zebra Finch had already been noticed and recorded in an earlier paper, but

in a very incomplete form. It was pointed out that if a male had built a nest and wanted a female to join him at it, or if a male and female were prospecting together for a nest, a characteristic set of actions was observed : " After the initial period of vigorous courtship, the male flies to a clump of twigs and moves round and round over it in repeated turns giving the nest-call and maintaining a special posture. This posture consists of fanning the tail and holding the body in a horizontal position. The legs are bent so that the body is kept low over the twigs. The beak is opened and shut extremely rapidly". It was noticed that this ceremony was typically followed by the building of a nest on the site, and it was felt that, although it functioned as a pairing ceremony, it was essentially linked to nesting behaviour. Only when colonies of Zebra Finches were studied in larger aviaries recently, was it found that the pairing and not the nesting was the essential feature. The ceremony could occur, it was found, with or without reference to a nest or nest-site, but never without reference to a pairing problem. Its relationship to nesting problems is, in fact, probably only an artifact caused by the intimate relation in the time between the setting up of a reproductive nest and a reproductive pair-bound.

The description of the pairing ceremony given above was found to be incomplete when Zebra Finch colonies were studied, more intense versions of the pattern being seen when mating " triangles " developed. If a mated male, for example, was beginning to ignore his female and chase another, his mate would follow him around giving a very elaborate version of the pairing ceremony. There was no reference here to a nest or nest site, but only to the male. Furthermore, the male had to be actively interested in the other female to produce this display in the mate, or at least, he had to be actively disinterested in the latter. The performance was seen in both sexes and males who were losing their mates were just as likely to follow them around giving the display. The following observation notes give a detailed description of the performance :

In a particular colony, one male had lost interest in his mate and was being helped at the nest by a new female. The old female was closely following the male around and also attacking the new female whenever she emerged from the nest. Neither the new female, nor the male, attacked the old female, but the latter was repeatedly assaulting and attempting to drive away (from the male) the new female. This basic situation developed as the new pair-bond became stronger and the new female finally began to attack the old one. The end came when the male joined in these attacks and the original mate was then finally ousted after the loss of a number of feathers. During all this time (several days) the old female was constantly performing the high intensity version of the pairing ceremony and this was always oriented to the male. It frequently developed into an attack on the other female ; for example, this was observed nine times out of a series of twenty-six displays noted at random. The less notice the male took of the old, displaying, female, or the more notice he took of the new female, the more intense was the display. It took the following form : " horizontal pivotings frontally or laterally towards the male, with mandibulations and tail-fanning and wing-drooping ; latter two movements occur one or two per second and wings and tail droop open and

fan open synchronously ; the flank feathers are fluffed right out, all the ventral feathers are raised, and the female squats on the perch in a crouched horizontal posture. Each time the wings give a rhythmical droop, the flank feathers are pushed out from the body, as the wings are inside them. There is a soft to loud rasping call that accompanies the display and which is like the high intensity nesting call. The eyes are repeatedly, but not rhythmically, closed and opened, and when open are still half-shut most of the time ; the head may even be turned round into the back in the typical sleeping position. This can occur at high intensity display moments and gives the distinct impression of being a displacement activity. The false nature of this apparent sleepiness is repeatedly revealed by the way in which the displaying female often stops her displaying suddenly to rush at the other female, springing into action from an apparently sleepy condition. The display can be given at one of three main intensities—Mandibulate ; Mandibulate and Tail-fan ; Mandibulate, Tail-fan and Wing-droop. The wing-drooping has not been seen before, and only appears at the very highest intensities. The lateral swinging, when in the horizontal posture, drops out typically at these higher intensity levels and is usually associated only with the simple and more sleeked horizontal-manbibulation displays. The mandibulations in this species, as in the Long-tailed Grassfinch, are very frequent indeed and normally audible from a distance of six feet ".

The above description gives a fairly complete picture of this particular pattern and it only remains to discuss its significance. Firstly, it must be stressed that this is a pattern which does not co-vary in any simple way with any basic level of sexual motivation in the performer. The female in the case described here was, in fact, being followed around herself at the time by another male who was repeatedly trying both to copulate and to pair with her. He failed completely during the period when she was giving the displays and was either ignored altogether, or occasionally attacked. All this time, the female was following the other male around and orientating her displays to him, despite the fact that he had long ceased to perform any sexual action whatever towards her. Considering these facts, one is forced to postulate a distinct pairing ceremony independent of a copulatory tendency.

The apparent derivation of this pairing display is most unexpected, for it is strikingly similar to the sun-bathing pattern of this species. In the latter, the bird crouches, half closes the eyes, or opens and shuts them, fans its tail and synchronously droops its wings. The tail-and-wings action is highly characteristic and identical with that seen in the pairing display. The rhythmic opening and closing of the wings and tail may, however, reach a higher intensity in sun-bathing, with a sustained opening of both. The wings may then be spread right out in a way not seen when pairing, but this posture is taken up not in a single action, but after a series of rhythmic openings and closings. The head may also be twisted round as in sleeping and in the pairing display. In both cases, the tail-fanning appears to have a lower threshold than the wing-drooping, and in the photograph in Pl. 2, fig. 5, low intensity sunning is shown, illustrating this stage. (In this photograph the posture of the bird is not particularly horizontal, but this was probably due to the

rather unusual circumstances necessary for taking the picture.) The feathers are ruffled in sun-bathing, but this element is missing from most pairing displays. Mandibulation was, however, seen during sunning bouts, apparently as a response to the heat, but this action can, of course, be caused by a number of quite different conditions.

The physiological basis for the similarity between sunning and the pairing display is intriguing, but is beyond the scope of the present paper. In the present context, the essential point about this whole complex is that it occurs in the Zebra Finch and that fragments of it have also been seen in the Long-tailed Grassfinch, but nowhere else in the Estrildinae. This suggests a relationship between these two species, but it must be borne in mind that it may only represent an insufficiency of observation with the other species. This criticism can only apply in certain cases, however, for detailed observations have been carried out with several other species, such as the Bronze Mannikin, for example, where it can be quite certain that this pattern does not occur. In this last species, circumstances were studied in which one would have certainly expected the pattern to appear in an intense form if the species possessed it, but it was never seen. On the other hand, it seems likely that certain close relatives of the Long-tailed Grassfinch, such as the Parson Finch, will also possess this display pattern, but further study is needed here.

7. *P. bichenovi* (Bicheno Finch). N. & E. Australia

Cayley reports that " The mating display is more subdued than that of the Zebra Finch and consists of a sequence of bobbing up and down movements by the male as he chases his mate around the aviary ". Unfortunately this description is completely ambiguous, because, from personal observations, it is clear that the " bobbing " referred to here probably relates to the extremely frequent displacement beak-wiping of this species. No other estrildine studied to date has ever shown such high frequency displacement beak-wiping. As many as eighty-three beak-wipes were recorded during the first five minutes of courtship after a female was introduced into the cage of a male, and this figure is not unduly high for this species. The male assumes a courting posture in which the plumage is fully fluffed, so that the body appears spheroid, with no special differential erection of the feathers of the type found in most other species. The bird crouches over the perch, parallel to the female, with his head twisted towards her. In this position he sings and beak-wipes ; in order to perform the latter, he does not have to move as far as he would if his courting posture was similar to his more usual generalised stance. It seems as if the posture is itself part of the beak-wiping ; the bird performs the action so many times, that he never, so to speak, quite straightens up again, until after the whole courting phase is over.

No dance movements were seen in this species, so that the " bobbing " referred to by Cayley may, in fact, refer to a vertical dance-step which is possessed by this species, but which was not occurring in captivity. The use of the ambiguous word " bobbing " is therefore particularly annoying here.

(For a photograph of the courting posture of the Bicheno Finch, see Morris, 1956 a.)

There are two call notes in this species : " Lost-calling " which is a plaintive twoooo-twoooo, rather like the calling of the Long-tailed Grassfinch, and " social-calling " which, like the song, is similar to that of the Zebra Finch, but higher and thinner in quality.

8. *P. modesta* (Cherry Finch). E. Australia

Butler (1899) reports that " its song has the almost voiceless character of the majority of the typical grassfinches, and its manner of singing is precisely the same ; the neck is elongated, the head projected rather downwards than upwards, the mouth opened widely and emitting a faint humming sound, not audible at all when other birds are singing ". From this account, from the fact that this species is now known to have mannikin-like lines on its nestling palates, and from the nature of its adult plumage markings, with the striking lateral barring, it seems highly likely that this species has strong affinities with the typical Mannikin group.

Little more is known about this species, with the exception of one interesting fact. Butler describes what appears to be a distraction display, thus : " . . . I purchased a second pair, and in May they built, the first egg being deposited on the 7th May. The hen was very nervous, and left the nest at the least alarm, tumbling about on the earth as if wounded, and gradually retreating from her home until about two yards away, when she hopped up into a bush and sat quite still ". As far as I know, this is the only instance on record of an estrildine performing a distraction display.

Subgenus *Poephila*

9. *P. cincta* (Parson Finch). E. Ausutralia

This species differs hardly at all from the next (the Long-tailed Grassfinch), except for beak colour, tail length, and song. The beak here is black, the tail short ; in the next species, the tail is long and the beak red. The song of the two species kept in captivity during the present study were quite different, that of the Parson Finch being even lower in pitch than that of the Long-tailed Grassfinch. The call-notes were also very low in pitch and much more prolonged than those of other species. Butler (1899, p. 177) gives a very accurate musical scoring of the song of the Long-tailed Grassfinch. Unfortunately he calls it the song of the Parson Finch. All the Long-tailed males I heard singing gave exactly the kind of song as that reported by Butler for the Parson Finch and the one male Parson Finch that sang repeatedly in my aviaries always sang a quite different song. Both the Parson Finches and the Long-tailed Grassfinches I studied were wild caught birds, so that no special distortion of their natural songs would be expected. I therefore conclude that Butler must have made a mistake in this case.

In behaviour there is little detectable difference between the two species. Both have a specialised head-jerking signal, which is not seen elsewhere in the estrildines. This occurs most during courting, or other social encounters. It also occurs at other times when no special activity is involved and appears to have acquired an extremely low threshold. The action is typically performed

immediately on landing and consists of a few very quick vertical stretchings and retractions of the neck. The rest of the body, tail, and wings, do not move and it seems as if the " excitement " flicking of the tail which occurs in so many other species, has been transferred to the head here. In courting situations, the head-jerking becomes so rapid and so frequent that it becomes quite divorced from landing and taking-off. Whereas in mild social situations, it only takes place with a landing, or some other definite form of locomotion, in intense social situations it can go off repeatedly without the bird moving at all.

In the Parson Finch this head-jerking seems to be less intense than in the Long-tailed Grassfinch and much less frequent, but only four birds of the present species were available for study, so this comment must remain a highly tentative one.

The courtship posture of the singing male involved a ruffling of the crown and head feathers, a strong erection of the black bib, and a general body fluffing. Both sexes beak-wipe repeatedly during the courtship. The body posture of the male when displaying is rather crouched, but possibly at higher intensities, which were not seen, this changes (as it does in several other species).

10. *P. acuticuada* (Long-tailed Grassfinch). N. and N.W. Australia

There is little to add about this species to what has been said above. More details were observed here concerning the nature of the feather erection of the head whilst singing. The crown feathers were fluffed like the rest of the body whilst the males performed their solitary non-courtship song, but became ruffled whilst actually courting. The extent of this ruffling varied from case to case. Sometimes only the posterior crown feathers and the nape feathers were ruffled, giving the head feather-posture a striking resemblance to that of the courting male Zebra Finch. But often the ruffling spread further forwards, so that the whole crown region was fully erected in a way not seen in the Zebra Finch male when courting.

Displacement beak-wiping occurs frequently during courtship bouts in this species, as in the last one, and both pivoting and inverted curtseying were seen here. They were not particularly exaggerated, as in some of the mannikins, but this may have been the result of low intensity displaying again. The lateral and the vertical movements were combined in a one-to-one ratio, to produce a complex rising-and-turning action. Once, this latero-vertical dance was seen to be performed by a male without reference to a female, the latter being in a different part of the aviary at the time. The male in question gave the display whilst holding a long straw in his beak, but gave it silently. This performance, of a dance without a song, is most unusual amongst estrildines.

The song of this species can best be conveyed by the following : tu-tu-tu-tu-tu WOO WAH WEEEE. The length of the last WEEEE note varies from individual to individual, but this particular sound is extremely similar to the high pitched WEEEEEEEE which ends the songs of several typical mannikins (see below) and along with the nestling palate-lines of the Long-tailed Grassfinch, may well point to a rather close relationship between this species and the

mannikin group. The distinctive lost-calling of this species can best be rendered by : We-WOOOOOH We-WOOOOOH.

One aspect of the behaviour of the Long-tailed Grassfinch which is shared, not with the mannikins, but with the Zebra Finch, is the pairing pattern. The detailed description given for the pair-formation behaviour of the Zebra Finch, included horizontal mandibulation with lateral twistings of the body, and rhythmic wing-dropping, as elements of the display. These were also seen frequently in the present species whenever new social relationships were developing. The wing-drooping appeared without tail-fanning in these cases (see Pl. 2, fig. 6) and it seems that there is a threshold difference between the two species, the Zebra Finch having the tail-fanning at a lower threshold than wing-drooping and the Long-tailed Grassfinch having just the reverse. Both, however, have horizontal mandibulating with lateral swinging of the body as the pairing response with the lowest threshold of all. (Many other species of estrildine have this mandibulating action as a signal in social situations of one kind or another, but its association with this special horizontal swinging from side to side has only been seen in the Grassfinch and Zebra Finch).

11. *P. personata* (Masked Grassfinch). N. Australia

This species is a close relative of the last two species and together the three species, with their various races, make a small natural group (which seems to me to be suited ideally to the status of subgenus, without the inclusion of the next species, the Gouldian Finch, as suggested by Delacour).

Its markings, structure, and deportment generally, relate it most closely to the last two species, as stated, but it is interesting that its call-note is virtually identical with that of the Zebra Finch. These two species answer one another's call notes and often select one another to clump with when in mixed collections.

12. *P. gouldiae* (Gouldian Finch). N. Australia

This is undoubtedly one of the most colourful of all finches and its plumage contrasts strikingly with the other members of this subgenus. It has a thin point to the centre of its tail, which is very reminiscent of the Long-tailed Grassfinch (see Pl. 2, fig. 6) and it has the heavy build and general carriage of the last three species. It does not, however, have their lined nestling palate markings, but spots, and in addition the nestlings possess elaborate, brightly-coloured, lobes and warts at the nestling gape. Its voice, too, is different and the song consists of a comparatively structureless hissing-whispering. During the solitary singing, the bird shows no special feather erection, although the feathers do seem to be slightly fluffed. The head is twisted and turned with the singing, but not in any special plane, as it is in certain other species. The beak is not opened appreciably during the song and there is no set beginning or end to any phrasing (or, if there is, it is far less obvious than in any of the other species, except the Cutthroat Finch).

One curious display which was seen in this species was " looming ". This occurred when a male and female were kept together and it consisted of the male looming over the crouched female. His body stretched right out over

her in such a way that his intense purple breast patch was pushed right in front of her eyes. In this posture, almost touching the female, the silent male would remain rigid for some time. This was seen on a number of occasions, but nothing was ever seen to develop from it. It is a similar phenomenon to " peering " in the Spice Finch (see Moynihan & Hall, 1954), but the latter is less static and is only performed to a male and then only when he is singing. The peerer stretches forwards with elongated, sleeked, body and (as can be seen from Pl. 5, figs. 19 and 20) gazes at the performer. This it does until the wretched singer gives up and either flees, attacks, or just sits quietly. Sometimes several birds peer at one singer. Moynihan & Hall report that the other males and females which are not the mate of the singer, may peer, but not the mate. These characteristics make peering rather different from looming, but it cannot be denied that it is a related phenomenon. The exact nature of the relationship would be easier to discuss if the function of either were known, but, to date, no functional explanation has been forthcoming. Thus far, peering has been noted for several species (Star Finch, Chestnut-breasted Mannikin, Chestnut Mannikin, Striated Finch, Spice Finch, Silverbill, and Cutthroat Finch), but looming has not been observed anywhere but in the Gouldian Finch. (As a matter of interest, two species in which peering definitely does not occur are the Zebra Finch and the Bronze Mannikin).

A report by Gilbert (1955), however, reveals that peering as well as looming may occur in the Gouldian Finch : " It is most amusing to watch a young cock with neck outstretched and huddled up closely to another youngster going through his singing exercises, his companion listening intently the whole time. These singing and listening performances alternate from bird to bird ". This is, of course, a perfect description of peering and indicates that probably, in this species, the looming display is a special form of a more typical peering display.

The only records of the more basic courtship song and dance performance for the Gouldian Finch come from Gordon (personal communication) and Risdon (1953). Gordon considers the Gouldian to be quite distinct from all other Australian finches and states that, when the male displays to the female, he " Stands erect, facing female, head back, bill in, throat puffed out in song, body feathers sleek, tail pulled well under, legs straight, ' dances ' with quick jerky springs, beginning with slow vertical jerks, the tempo quickening until the feet leave the perch in rapid tattoo of half-inch springs. The ' dance ' is performed for quite some length of time for so small a bird, and is followed by mating ". He points out that, although the call note of this bird is loud, the song is inaudible from a few yards away. Gordon also reports that the female " Stands close to the male. Body feathers sleek, neck and head bowed, head shaking, tail down and pulled to side toward male—this stance is held from the time the male begins till ' dance ' ends, and the female bends to the horizontal ".

The vertical dance of the male described above is similar to the inverted-curtsey dance of other species, but the head and neck movements of the female seem to be unique to the Gouldian Finch.

Riscon (1953, p. 57) states that the male of this species " starts his display by dancing up and down on the perch before his hen, expanding the black or red feathers on his face and the purple ones across his breast, the while uttering his whispering song. Then suddenly, depressing his beak on his chest he bows right forward till his face almost touches the perch. This generally ends the display, but sometimes he will draw himself up to his full height and repeat the performance ". The bow that is mentioned here sounds like a rather ritualised form of displacement beak-wiping.

13. *Erythrura* spp. (Parrot Finches)

The nine species of very brightly coloured Parrot finches can be discussed together here. Delacour says that they " form an isolated group, with no great affinities for the other Estrildinae " (in which case it is rather ironic that the Grassfinch tribe should be named after them). Hardly anything is known of their behaviour. Superficially their bright colours remind one of the Gouldian Finch, but this is probably a convergence, and Delacour thinks that the similarities " do not seem to imply close relationship ". Nevertheless, it is worth pointing out that Cayley (1932) quotes a Mr F. Buckle (on the Blue-faced Parrot Finch, *E. trichroa*) as saying that " the young when first they leave the nest are a dusky green in colour ; they also have luminous nodules on each side of the bill, like the young Gouldian Finch ". Their affinities must therefore remain problematical until we know more about their behaviour.

The only fragments of knowledge we have about the behaviour of these birds, to date, concern the copulation of the Red-headed Parrot Finch (*E. psittacea*). King (1951) reports the observations of a Mr N. Nicholson that " It is, perhaps somewhat unusual that mating actually takes place on the nest ". Gordon (personal communication), however, reports that " Males drive females about, ' chase ' in rapid flights, catches female by back neck feathers, hangs on while mounted, similar to domestic fowl-rooster ". These two observations appear to be contradictory, but it is quite possible that both occurrences are common in this species*. I have observed nest-copulations in the Bronze Mannikin, but have not seen neck-gripping by a mounted male in any estrildine species under normal conditions. (It was seen, however, also in the Bronze Mannikin, when an injured, flightless, individual was mounted on the ground, but this appeared to be rather abnormal). Gordon makes a brief mention, in his report on the Gouldian Finch that " Mounting males get balance holding female's neck feathers . . . ", so that it is possible that this activity may be typical of this species as well as the Parrot Finch.

B. Mannikins :

Genus *Padda*

14. *P. oryzivora* (Java Sparrow). Java and Bali

One of the largest estrildines, this species has been separated generically because of its markings, which include a pink beak and vivid black-and-white head, and its morphology.

* Nicholson (personal communication) has now confirmed this.

Butler reports that, when courting, the male " bends his body like an arch over the perch, turns his head sideways towards the female, and lifts himself jerkily up and down, singing all the while, and gradually sidling up to his mate ". From this account it is clear that this species had the " low twist " posture discussed by Moynihan & Hall (1954) for the Spice Finch ; also, that it shows the vertical inverted-curtsey dance movement.

The song is discussed at length by Butler (1899), but the one important comparative feature of it is that it possesses (at least, in the birds I studied) a high-pitched, thin, long drawn out, WEEEEEEEE whistle at the end of each phrase. This particular note, recorded so far in this paper only for the Long-tailed Grassfinch, is one of the most important estrildine sounds, from a comparative point of view. It occurs in a number of species in exactly the same form, always at the very beginning or end of the song phrases (where these are being repeated over and over again, it is difficult to tell whether it starts or ends the song, because the very first notes are often missed, and because the song may end abruptly in the middle of a phrase). I have so far noted it in the song of the above mentioned species and also the Chestnut-breasted, Pale-headed, and Chestnut Mannikins. It is one of the few distinct song characteristics that exist amongst the estrildines. The songs of these birds appear to be the least conservative characters of all, for, even with visually very similar species, such as the Bronze and Black-breasted Mannikins, or the Parson and Long-tailed Grassfinches, the songs are strikingly different. This particular whistle, however, has for some reason been a much more conservative character and this suggests that the Java Sparrow (and perhaps even the Long-tailed Grassfinch) are offshoots from the more typical Archipelago Mannikin forms. This suggestion is, of course, extremely tentative, and we need to know a great deal more about the behaviour of these birds before a more definite idea can be formed.

Genus *Amadina*

15. *A. fasciata* (Cutthroat Finch). West, Central and East Africa

Several short papers have already appeared on the behaviour of this species (Morris, 1954 b, 1955 c, and 1956 b). Its sexual patterns will therefore only be described briefly here.

The male assumes a very vertical posture during courtship, with beak horizontal and not appreciably opened. The head pivots smartly from side to side whilst singing. There is extreme ruffling of the feathers in a special way (see illustrations in Morris, 1955 c, 1956 a and 1957 a). The throat is not erected but the extent of the erection increases towards the brown belly patch. There is a sudden increase in the extent of the erection at the white edge to the belly patch, which helps to exaggerate this latter marking when the bird is displaying. The feathers of the crown, nape, and all down the back, are ruffled. The bird dances to the female with either inverted curtseys or with lateral pivots. The curtseying is by far the most common display movement, and the pivoting has only been seen once or twice (since the previous papers were written). The typical one-to-one combination of these two

movements has not been seen in this species. When it made one movement, that bout of courting did not include the other type. Probably, if the behaviour of this species were better known, the combination would be seen. The display of the male is often given with a long straw in the beak, but not always so. The use of a straw in this and other species, during sexual displays, never seems to be obligatory.

16. *A. erythrocephala* (Red-headed Finch). South Africa

This species is extremely closely related to the last. Little is known of its behaviour, but Buttner (1950) reports that " The Red-headed Finch breeds freely with its relative, the Ribbon (Cutthroat) Finch ; in fact, cocks of the latter species will invariably rob the Red-heads of their hens when the two kinds of birds are housed in the same aviary ".

Genus *Lonchura*

Subgenus *Heteromunia*

17. *L. pectoralis* (Pectoral Finch). N. Australia

Cayley says " In habits they differ somewhat from the true Mannikins, being rather shy, keeping to themselves, and spending most of their time on the ground. . . The mating display of the male is very similar to that of the Crimson and Star Finches with the addition of the straw-carrying habit of the Mannikins ". Delacour also considers this in many ways to be " an intermediate between the grassfinches and the mannikins ". It must be admitted that it has more complex markings than most Mannikins, but a close scrutiny of such characters as its face-mask (as already pointed out) and various other features of its plumage leave no doubt as to its affinities with the other two Australian mannikins proper (the Chestnut-breasted and the Pale-headed). A number of its peculiarities can be accounted for by the fact that it has taken to ground living. Gordon (personal communication) reports that " Males hold a short straw while displaying around the female in strutting jerky hops. Done upon ground, tail fanning the dust—not unlike the domestic pigeons ". Mackie, quoted by Cayley (1932) confirms this tail-fanning of the displaying male, thus : " The male is most conspicuous and during the mating season is constantly dancing around his mate, fanning out his tail, and carrying a long straw or grass-stem in his bill. He has a low song which is difficult to hear in a large aviary ".

Subgenus *Euodice*

18. *L. malabarica* (Silverbill). Tropical N.W., Central and N.E. Africa, S. Arabia, Persia, Afghanistan, Baluchistan, India and Ceylon

The song posture of the courting male of this species (see Pl. 2, figs. 7 and 8) differs from that of all the other mannikins studied. The most characteristic difference is that here there is no fluffing of the ventral feathers. The neck is fully stretched and slightly arched, with the throat a little expanded. The beak is not opened appreciably and is horizontal. The male assumes a vertical

posture, but leans slightly towards the female. In this posture, lateral pivoting was seen without any vertical movements. In other cases, a more horizontal posture was held by the singing, courting, male and, whilst holding a straw in his beak, he then performed the vertical inverted-curtsey dance movements, but without any lateral pivoting. (Again, though, the two movements are probably combined in high intensity displays.)

Displacement beak-wiping and preening were both seen. The male also showed a highly modified version of displacement beak-wiping, in which the head and and neck made U-shaped movements rather quickly, accompanied by mandibulating, just before a bout of singing began. The bird assumed the courtship posture, mandibulated and made U movements, and then began immediately to sing. To the song was then added the pivoting in certain instances. This sequence, as we shall see below, is very similar to that of the courting male Striated Finch, except that the latter moves down in a much more exaggerated dip when mandibulating. During the Silverbill courtship the tail is markedly twisted towards the female (see Pl. 2, fig. 7).

The song of the Silverbill is quite unlike that of any of the other mannikins, being clear and pure instead of harsh or rasping. In this respect it is, in fact, reminiscent of the waxbills and Butler (1899) goes as far as to say " If the Silverbills looked up to heaven to utter their shrill song, I should unhesitatingly declare that they were aberrant Waxbills . . . " However, their dull coloration, their markings, and lined nestling palates seem to justify their present position.

Subgenus *Lonchura*

19. *L. bicolor* (Black-breasted Mannikin). Ethiopia south to Angola, the Belgian Congo and Natal

This diminutive African mannikin is a very close relative of the next species, the Bronze Mannikin and Butler says simply that the male " dances and hums in the same manner " as the latter. This is not completely true, for, although the movements do all appear to be exactly the same, the song is quite distinctly different.

20. *L. cucullata* (Bronze Mannikin). Ethiopia

This species has been dealt with in detail in a very recent paper (Morris, 1957 b), and its behaviour will therefore only be briefly summarised here :

Male courtship performed with beak open wide, tongue protruding : beak points downwards ; body feathers ruffled except for throat region and head : legs bent ; tail twisted to female ; inverted curtsey dance at low intensity, with pivoting added in at higher intensities ; displacement beak-wiping absent almost entirely and its place taken by displacement preening ; no straw carrying ; no low twist ; no peering ; mandibulating immediately before each song phrase, but not accompanied by dipping or bowing.

The female quivers her tail in ruffled oblique posture instead of usual horizontal sleeked posture. If the male is not ready to copulate, he performs leapfrog sequence, vaulting back and forth over the female, with a quick displacement preen between each vault.

There is a nest ceremony in this species, related possibly to the pairing ceremony mentioned earlier for the Zebra Finch. However, this display is built entirely of elements taken from the nesting repertoire and is never performed away from a nest site, whereas the Zebra Finch ceremony is derived from the sunbathing behaviour pattern and may or may not be associated with a nest or nest-site. The Bronze Mannikin nest ceremony certainly appears to strengthen the pair-bond and some elements of it re-appear in the pre-copulatory ceremony just described. The nesting ceremony includes ritual scooping, mandibulating, gaping and tongue-protruding and, on occasion, was even seen to lead to copulations in the nest. But for full details, see Morris, 1957 b.

This species, along with the Black-breasted and Magpie Mannikins, appear to form a natural small group of African mannikins. The Magpie Mannikin is only included here, however, because of its very similar markings and colours, and it would be most rewarding to make observations on its behaviour.*

21. *L. striata* (Striated Finch). Ceylon, India, Burma, Siam, S. China, Indochina, Malay Peninsula, Sumatra

This simply-marked, brown and white mannikin is better known in captivity in its pied domesticated form, the Bengalese Finch, or Bengalee (known in the U.S.A. as the Society Finch). Much has been written about the origin of the Bengalese Finch. It is supposedly a hybrid between the Striated Finch and various other species of mannikins. Most popular candidate for its other "parent" is the Silverbill. However, it has none of the Silverbill's behaviour patterns and all of the striated Finch's. This consideration, plus the fact that Bengalese Finches often revert to a non-pied type indistinguishable from wild Striated Finches, leaves little room for doubt that this domestic finch from the Orient, which has been bred in captivity for several centuries, is not after all a magic hybrid but only a mutant. (Also, five offspring from a Bengalese X Striated cross, bred in the laboratory, were all almost pure Striated.) The following remarks about the behaviour of the Striated Finch therefore apply to the Bengalese Finch as well (and, in all instances, the patterns have been observed in both).

In a medium or low intensity courtship the male has his belly feathers fluffed, his throat and crown feathers flattened, and his nape feathers ruffled; the legs are bent; the beak is horizontal and opens and shuts fast and exaggeratedly during the song. (This and the beak and head movements seen in other species are not however linked, for mechanical reasons of voice production, with the particular noises produced during the songs. If birds from one species are reared by another species, the young birds learn to sign the "wrong" songs of their foster-parents, but they still sing them in the postures and with the movements which are "correct" for their own species. This means that song characters and song posture and movement characters are independent and can, taxonomically, be considered separately.)

* This has since been possible, at the London Zoo, and the sexual behaviour of the Magpie Mannikin does confirm its inclusion here.

The tail is slightly raised, which is unusual. Most of the other estrildines keep their tails below the horizontal when courting. The male dances with small amplitude pivots, from side to side, through an angle of about 90 degrees. This medium to low intensity courtship is illustrated by the Bengalese Finch shown in Pl. 4, figs. 13 and 14. In Fig. 14 the male is seen pivoted away from the female and in Fig. 13 he has swung towards her.

In the higher intensity display, the feather erection is more extreme ; the white ventral feathers are now fully ruffled and so are the crown and nape feathers. The legs are less bent and the bird's body no longer touches the perch. It becomes more vertical and the tail is now almost horizontal. Inverted curtseys are added to the pivoting movements now, in a one-to-one ratio. The higher intensity display is illustrated by the wild-type Striated Finch male in Pl. 3, figs. 11 and 12. As before the right-hand figure shows the male pivoting away from the female and the left-hand one shows him turned towards her.

Before the courtship song and dance begins, the male performs bowing or dipping movements, accompanied by much mandibulation (see Pl. 3, fig. 9). In the extreme form (see Pl. 3, fig. 10) the result is a striking low twist posture. This differs slightly in form from that of the Spice Finch (see Pl. 4, fig. 16) and it is also sustained for a much shorter time than in the latter species. It is performed *before* the male assumes the characteristic feather posture in which he sings and dances. In the Spice Finch, the feather posture, the song, and the vertical part of the dance can all be seen to be performed by males in the low twist position, but this is never so in the Striated Finch.

It seems as if this initial courting posture has also been derived from displacement beak-wiping, as in the Silverbill, but this argument will be developed below.

22. *L. punctulata* (Spice Finch) Ceylon, India, Burma, S. China, Siam, Indochina, Hainan, Formosa, Philippines, Malay Peninsula, Sumatra, Java, Bali, Lesser Sunda Isles, Celebes

The behaviour of this species has been dealt with at length in a recent paper by Moynihan & Hall (1954) and their findings concerning the form of the male's courtship performance will therefore only be summarised briefly here :

There are two basic courtship phases. In the first, the male (and also, to a lesser extent, the female) hops excitedly back and forth with nest material in its beak. During this phase, there is much mandibulating and looping of the material. Then when the male comes near to the female he drops his straw and performs a number of beak-wipes in front of the female. Phase two begins when the male stops this initial beak-wiping and assumes the characteristic song posture (see Pl. 4, fig. 15). This is an exaggeration of the solitary song posture of this species. The latter involves an erection of the head feathers, especially those of the crown and chin, which are ruffled. The belly feathers are slightly fluffed. The beak is horizontal and more or less closed except for the final note of each phrase, when it is opened wide. The legs are bent, the bird's body touching the branch. The head pivots smartly from side to side. In the courtship song posture, the ventral feathers are more fully

fluffed, the tail is slightly more depressed and the rump region is strikingly fluffed (see Pl. 5, fig. 19). The flank feathers are typically fluffed outside the wings. The legs become more stretched and the whole body now begins to pivot from side to side. Moynihan & Hall also report that, in some of their males, there were vertical dance movements as well as lateral pivoting movements during this type of performance.

The vertical dance movements are more characteristic, in this species, of male courtships in which the male assumes the low twist posture. In this posture, the male's body is horizontal and the head twisted round towards the female (see Pl. 4, fig. 16). The feather erection and song occur as before, but the male in the low twist does not show any head or body pivoting. The vertical dance movements are now more exaggerated, and this type of display may occur, not just as a part of a sequence leading to the more upright version, but as an alternative to it. (Nevertheless, in some cases, the low twist display does lead to the other, as in the Striated Finch). Moynihan & Hall stress that the males performing the song and dance in the low twist posture were in a more aggressive mood than those performing it in the usual manner. This automatically links the vertical dance movements to a more aggressive mood than the horizontal pivoting ones. It is interesting to speculate whether this can explain the various specific differences connected with these characters.

The vertical dance movements appear in some species, where the horizontal ones are almost absent. In other species, the reverse is the case. Again, in some species, the vertical movements appear at low intensities by themselves and the horizontal movements are added on at higher intensities. Once more, the reverse may occur. Finally, in species such as the present one, either type of dance movement may be observed by itself, or both may be performed together. At the present time it is difficult to relate these specific differences to appropriate differences in aggressiveness during the male display. However, certain instances do bear out Moynihan & Hall's point. The Zebra Finch, for example, which is a horizontal dancer, is not typically very aggressive to the female, whereas the Bronze Mannikin, which is primarily a vertical dancer, is often very aggressive. As the male Bronze Mannikin's aggression subsides with sexual arousal, he begins to add pivoting steps to his dance. The Striated Finch, however, provides a difficulty, for sexual arousal here is accompanied by the addition to the pivoting dance of the vertical one. This may mean that the male of this species is too afraid of the female to begin with and has to reduce its fear as sexual arousal proceeds, thus leading to the more aggressive display. Alternatively, both the dance movements may have become ritualised to the extent that they are now emancipated motivationally and are simple sexual responses with different thresholds in each species. Until a careful quantitative analysis has been made with a number of species, of the relationship between the frequencies of the two movements and various attacking, fleeing and sexual elements in the courtships, it is impossible to carry this discussion further. The ideal species to use for such a study would be the Bronze Mannikin, the Striated Finch, the Spice Finch and the Zebra Finch, each representing a basically different type.

From a derivational point of view it can be said that the turning away from the female which occurs in the pivoting dance movements supports the view that there is less aggression in this than in the inverted curtsey. The pivot dance appears to have evolved from intention movements of fleeing from the female, whereas the inverted curtsey dance seems to be a ritualised sequence of intention movements of mounting (or, at least, of jumping towards the female).

Peering by the Spice Finch has been discussed earlier and it is illustrated in Pl. 5, figs. 19 and 20.

Three hybrids between this species and the Chestnut-breasted Mannikin were obtained from the Copenhagen Zoo, thanks to the kindness of Dr Holger Poulsen. These birds were nearer to the Spice Finch parent as regards their markings and colours and, interestingly, were also nearer to the Spice Finch in their singing posturing. The three individuals were males and all three sang in a manner quite unrelated to the songs of either parent. It emerged that they had been reared in an aviary containing canaries and were now doing their best, each in his own way, to simulate the exotic song of this fringillid. The extent to which one of them succeeded was remarkable, especially when the rasping, grating, squeaking qualities of the two parent songs are borne in mind. An unfortunate outcome of the extraordinary performance put on by the one male was that the great effort involved resulted in his whole frame vibrating so much that his tail quivered violently, thus inadvertently giving the female estrildine invitation signal, occasionally with disastrous effectiveness.

Subgenus *Munia*

23. *L. ferruginosa* (Chestnut Mannikin). Ceylon, India, Burma, Siam, S. China, Formosa, Hainan, Indo-china, Malay Peninsula, Sumatra, Java, Bali, Borneo, Philippines, Lombok, Flores and Celebes

The song of this species is particularly interesting. It has three parts to each song phrase. The first part consists of a slow clapping of the beak, which appears to be a ritualised version of mandibulating. Many species mandibulate just before each song phrase, like the Bronze Mannikin, and in the present species the rapid opening and closing of the beak appears to have been slowed down and increased in power to produce a primarily auditory display. This phase of the song phrase passes into an almost silent one in which the bird heaves up and down in a manner reminiscent of a human runner very out of breath. This in turn passes into the third phase which consists of one or several long, high, thin, drawn-out whistles. Each song phrase is very long compared with the typical (one second long) phrases of such species as Zebra Finches and most other grassfinches. The Chestnut Mannikin song phrase lasts as long as sixteen-and-a-half seconds in some cases, with eight seconds as a minimum. Variations in the length of the song phrase in this species are mainly dependent on how many ending whistles there are : the sixteen-and-a-half second case was a three-whistle affair, whereas the eight-second case only had one whistle.

The song posture, whether solitary or courting, involves the erection of all body feathers, with the exception of those of the throat and upper breast. The head is pointed down and the beak opened. There is no head pivoting, but a suggestion of a vertical nodding. The only dance movements observed were vertical ones, with no pivoting, and with no low twist. Displacement beak-wiping was common during bouts of courting.

24. *L. maja* (Pale-headed Mannikin). Malay Peninsula, Sumatra, Java, Bali, Lombok, Flores, Celebes, New Guinea, and N. Australia

According to Butler, "the male raises himself laboriously, stretches his head obliquely upwards, spreads his short tail and commences an extraordinarily zealous song in which one sees beak and throat in most industrious motion, but which is not accompanied as in the Cutthroat Finch by an up and down hopping dance, but only by a gentle and almost automatic movement of the head from side to side". From my own observations of two races of this species (the White-headed Mannikin and the Australian Yellow-rumped Mannikin) I cannot agree with Butler in all these points. The male certainly stretches his neck upwards, but Butler gives the impression from his wording that the beak is pointing upwards, when, in fact, it points downwards as in the last species. Also, the tail is not necessarily spread during song. Finally, the absence of the vertical dance movements in Butler's birds was undoubtedly due to the absence of high intensity responsiveness, rather than to the complete absence of this component in this species.

Mandibulation and displacement beak-wiping occur prior to courtship singing in this species and nodding accompanies the song. Butler is quite wrong to suggest that there is any head pivoting during the song. Also, there is not exactly a great deal of beak movement, the beak being held wide open most of the time while singing. There is general feather erection all over the body except in the throat and upper breast region. In other words, this species behaves when singing very much like the last, even including the same kind of long drawn-out whistle at the end of each song phrase.

25. *L. castaneothorax* (Chestnut-breasted Mannikin). Australia and New Guinea

A close relative of the last species, with very similar song, including the long whistle at the end, the head nodding, the heaving, the absence of head pivoting, the downward pointed beak, the wide-open mandibles, the stretched neck, the fluffed out body feathers, and the displacement beak-wiping. In addition, a low twist display was seen in this species.

A typical introduction involved the following stages: both birds shake; male sings in low twist but no dancing; both birds mandibulate and then beak-wiping (double wipes); both ruffle and give repeated single wipes; male does song and curtsey dance in oblique posture (i.e. semi-low twist); other bird peers at, then preens, the singer.

The song is one with a complete 4-phasic phrase: weeeeee eeeeeeeee/tuee tuee tuee tuee tuee tuee tuee tuee tuee/cheeouk cheeouk cheeouk cheeouk cheeouk/ching-ching-ching-ching-ching. The long thin whistle

(weeeeeee) occurs at the beginning of this song phrase and it is possible that this is also the case with the other species possessing this note. Unfortunately, this note is often the one which ends a bout of singing as well as beginning it and since the first notes of a bout are often missed, it is difficult to be certain. The important point, however, is that this note is extremely characteristic and quite identical in the several species which possess it. Silent mandibulation preceeds each phrase.

C. Waxbills

Genus *Estrilda*

Subgenus *Estrilda*

26. *E. temporalis* (The Red-browed Finch). E. Australia

As stated earlier, the waxbills are not being included in the present paper, but the Red-browed Finch is an exception, since it is in doubt as to whether it is a true waxbill or not.

The inconsistency in Delacour's system, concerning this species, has already been pointed out. He has called it a waxbill mainly because it looks like one (the Red-eared Waxbill) and because it displays with its beak pointing upwards and singing a high-pitched song. But the Crimson Finch looks like the Firefinch (a waxbill from Africa), the Painted Finch points its beak upwards when singing, and the Star Finch has a high-pitched voice. Yes these three species are all considered to be good grassfinches. Even if it is pointed out that the Red-browed Finch has *more* waxbill-like characters than these other species it is still perhaps advisable to be cautious over including a single Australian form in a predominantly African group. Its sexual behaviour is as follows :

The solitary singing posture of the male involves a ruffling of the ventral feathers, but no erection of any other region of the plumage. The bird sings with rather stretched legs and upright stance, the beak being horizontal and not opened appreciably. The head appears to make slight lateral movements while singing. The song is little more than a rhythmic repetition of the call note. Each song phrase consists of three or four call notes spaced in a special way. In one individual male, the spacing was as follows : teee-te-tee teee-te-tee, and so on. In another male it was : teee-te-tee-teee teee-te-tee-teee teee-te-tee-teee. This is undoubtedly the simplest song in the Estrildinae and indicates the probable way in which singing was evolved. First the simple call note of the species is repeated over and over again, then it develops a special spacing as in the present species, thus giving rise to simple little song phrases. These can now act as units themselves and can develop further, more complex, relationships, and so on, until one arrives at the more complicated song phrases of most other species.

Two quite distinct sexual displays were seen in the Red-browed Finch and the relationship between them is still not clear. Both displays appeared to be leading to copulation, but there was no sequence involved. On one occasion a male would give one display type, and on another he would perform the

second type, but no clear-cut causal difference could be found. The only clue was that the first type of display was seen mostly at the time when the new birds were introduced to one another. Later, when the group was stabilised in its aviary environment, only the second type was recorded.

When the first introductions were brought about, the immediate effect was to produce a special posture in the male. His body became horizontal and his tail vertical, pointing upwards. He faced the female and showed repeated beak-wiping, his body " see-sawing " with the wiping actions. The front view seen by the female displayed the red regions of the male's body (the red streaks of the beak, leading to the red eye-brows, and also the red rump patch). This posture is very reminiscent of the Crimson Finch's threat posture, but the male did not attack the new-comer in this case. The beak wiping at this initial stage of the introduction was very fast but thirty of the wipes were scored and they were all doubles (wipe wipe). In the Zebra Finch, wiping at this speed and with this high frequency during courtship would certainly result in nearly all single wipe wipings (see Morris, 1954 a). The next stage in the behaviour can best be described by quoting from protocols :

" The second stage includes song with the beak wiping. The male adopts the horizontal, tail-up, posture and rocks up and down in see-saw fashion with the beak-wipes coming so fast one after the other that the ' up ' pause of the rocking is as short as the ' down ' pause. Again this differs from the Zebra Finch, where the up pause is much longer than the very rapid down pause. The high intensity courting of this kind in the Red-browed Finch involves very rapid double wipes at the bottom of the rocking movement, at an intensity at which the Zebra Finch would be doing exclusively single-wipes. However, at a higher intensity still, with the song becoming very loud and clear, the Red-browed Finch gives up the double wipes and begins to ' bow ' (i.e. it gives abbreviated single wipes). This higher intensity bowing-singing display is more broadside-on to the female, less frontal than the silent-bowing. And with this there is a change in tail position. The tail becomes less vertical and is more twisted round towards the partner. Finally, it should be stressed that, even in the up phase of this display, the male is extremely near to the horizontal ".

Later, a third basic stage in the courtship was recorded, but it was not continuous with the above. Rather, the male changed over after a time to this new type of display :

" The full song-and-dance display . . . The male selects a long straw, holds it in his beak, advances to the side of the other bird and begins to sing and dance with vertical movements. These are only slightly directed towards the other, the male being almost broadside-on. The body is now extremely erect, with the legs stretched and the head held back, the beak pointing to the sky. The vertical inverted-curtsey jumps are so vigorous that, as in the Gouldian Finch, the male's feet leave the perch each time. The tail is held more downwards now and is strongly twisted towards the female. This display attracts the female and she approaches the male. As she alights near him *she throws back her head* and, for a few moments, she holds this position with her beak pointing upwards like his. This display is extremely similar

to the head-tossing of the Painted Finch under similar circumstances. The movement is slower in the present species, but it is fundamentally the same. Also, the red-streaked beak markings of the two species are similar ".

A possible derivational explanation of the head-up display was provided by the following observations. Several times, a male was seen to be about to display to a female, but then instead went into the nest and incorporated the piece of straw it was holding into the structure. This was done with scooping movements and it was noticed that at the top of each scoop, the male's neck was stretched vertically upwards, his beak was pointing upwards and he was holding a straw in his mandibles. In all these respects the " up " posture of the scooping action was similar to that of the song and dance display posture.

Many species court with the beak up, many more with it horizontal, and many more again with it pointing downwards. They all scoop in the same way, as far as is known, but there is no reason why different groups should not have " frozen " the scooping posture at a different stage in different cases, the beak pointing downwards at the beginning of a scoop and upwards at the end. An alternative explanation would be that the bird is assuming a head back posture in the present species as part of the intention movements of flying away upwards, but this would be difficult to reconcile with the comparative evidence.

Taxonomically, I am convinced that the Red-browed Finch is a close relative of the Crimson Finch and the Painted Finch, and that, if it is a true waxbill and has resulted from an independent waxbill invasion of Australia, then the other two species are also waxbills. If they are not, it is not.

Parental behaviour

Parentally speaking, the estrildines are a very homogeneous group. Apart from the mouth markings already discussed, there is little of comparative interest in this aspect of their behaviour. In almost all species there are five small white eggs in a clutch, and the parents take turn in incubating them. Both male and female also share the task of feeding the young birds. The latter beg for food with a special twisted posture. The neck is not stretched upwards in the more usual fashion, but it is twisted tightly round so that the beak gapes upwards but at the same time leaves a space above it and below the roof of the domed nest. If the young birds stretched their necks upwards vertically they would touch the top of the nest and could not then be fed. The incubation period (two weeks), the nestling period (two weeks), and the fledgling dependency period (also two weeks), given for the Zebra Finch in an earlier paper (Morris, 1954 a) appear to be roughly constant throughout the group. The young birds mature extremely quickly, in about three months from fledgling, and will breed in their first year.

COMPARATIVE DERIVATIONAL PROBLEMS

Before finally reviewing the relationships between the various species, some general comments about the origins of the different sexual components must be made.

Specific differences in respect of the form of these components can easily be deceptive. Two closely related species may have diverged widely in their

sexual signals, or two widely separate species may have arrived at a very similar signal from quite different sources, simply because of the signal value of a particular type of movement or posture. An example of the first would be where two species both used displacement beak-wiping as a ritualised signal, the one "wiping" its beak back and forth without bending down, and the other bending down in a bow, but without making the wiping movements. If it can be shown that both actions have originated from the same movement, then their *superficial difference* dwindles in importance. An example of the second would be where two species both bow ceremonially to the female, but the bow is derived, in one case from beak-wiping, as above, and in the other from intention movements of taking-off. In this case, their *superficial similarity* dwindles in importance.

Such points as this must be taken into consideration when evaluating the ethological data in a comparative study. It is worthwhile here to run briefly through the main components of the various displays, noting their possible origins :

Straw holding is derivationally simple. Quite clearly it originates from the genuine carrying of nest material to the nest and has become involved in the sexual patterns because of the intimate association in time between the building of a reproductive nest at high intensity and the pre-copulatory phase. In some species, such as the Zebra Finch, straws are not used in display. In others such as the Spice Finch, the straw is carried about in the first stage of courting and then dropped when the bird begins to sing and posture. In others, such as the Star Finch and the Red Avadavat, the birds bow with the straws held in their beaks, but release them for the final stages of the displaying. In still others, such as the Red-browed Finch the bird retains the straw actually during the dancing stage of the display.

The intimate relationship between nesting and courting referred to above is of great importance in other respects also. It seems to give rise to more sexual display elements than any other aspect of the birds' behaviour. Mandibulation, which, during nesting, so typically accompanies the carrying of material, is seen in sexual situations in many species. In some, such as the Spice Finch, genuine mandibulation of material is seen associated with the straw carrying in the early phases of pre-copulatory patterns. But also, in this species, and many others, mandibulation occurs without any object being held in the beak. In the Zebra Finch and the Long-tailed Grassfinch this is typically performed in the special horizontal posture associated with pair formation ceremonies. In other species, it is performed in a low dipped posture (Striated Finch) just before the song begins, or in the ordinary song and dance posture itself. In the latter cases, it is usually seen immediately before the start of singing. In a number of cases, the mandibulating appears briefly before each song phrase in a bout of singing (e.g. Bronze Mannikin). In different species, the movements of the beak which accompany the song, appear to be exaggerated forms of mandibulating. At first sight, one gets the impression that they are essential to the mechanics of voice-production and that differences in the sounds produced by the different species account for their variations. However, rearing birds of one species with those of another reveals that this is not so

and that one song can easily be sung with quite different beak movements. I suggest therefore that many of the singing beak movements are derived from mandibulation. In the case of the Bronze Mannikin, the beak is held open while singing and the tongue is protruded and quivered. The opening and shutting of the beak which occurs in mandibulation appears to have "frozen" here at the open stage. The tongue component is probably similarly derived, since tongue movements are employed when mandibulating nest material; the material is moved about in the beak by the tongue, which appears to test the texture of the grass or straw. In the Striated Finch, the exaggerated opening and closing of the beak shows a modification of mandibulating which involves a slowing down of the opening and shutting actions and an increase in their amplitude. In the Chestnut Mannikin, these movements are also slowed down, but here the beak is shut with a greater force, producing a clapping noise, which virtually becomes part of the song itself.

As already discussed, the nesting action of scooping seems to be used in determining the head and neck posture, some species tilting the head down and others up.

Bowing displays, as stressed above, may have different origins, and this component of the Star Finch display appears to have been taken from a different source from most others. Here the form of the movements indicates that this display pattern comes from intention movements of flying away, presumably to the nest with the straw held in the beak. The bowing of other species mentioned in this paper (with the exception of the Red Avadavat) has evolved from displacement beak-wiping.

This last named action must now be considered as a source of signals. It appears in many species and is comparatively unmodified in some. Even where specialised versions of it appear, it is interesting to note that the unmodified action can also take place as a displacement activity and has not been completely replaced. In the Zebra Finch incomplete beak-wiping appears in several forms. The extent of the bending down may be reduced, the number of wipes per wiping reduced, their speed increased, the orientation of the bird to the perch abandoned, and so on. In various other species, one of these modifications has become the typical one. In the Silverbill, the lateral wiping movements are retained in a simplified manner, but the bending down has vanished, resulting in a simple U-shaped action of the head. In the Chestnut-breasted Mannikin, the lateral elements have gone and the bending down is shallow, resulting in a slight bow which is little more than a nod. In other species the bending down has become exaggerated but the wiping element has gone. This occurs in the Striated Finch and gives rise, when the down posture is sustained, to the low twist posture. In the Spice Finch this low twist posture is maintained for long periods and is performed simultaneously with the song and dance. The photographs in Pl. 5, figs. 17 and 18 show the relationship between the displacement beak-wiping action of the Zebra Finch and the sustained low twist posture of the Spice Finch. The Zebra Finch does not sustain its down phase of its beak-wiping movement, but the electronic flash photograph "freezes" the movement here. The low twist of the Spice Finch is "frozen" by the bird itself and, when these two pictures are compared, the

great similarity between the two postures makes it easy to believe that the sustained one has evolved in the way suggested here.

The origin of feather postures has been discussed at length in another recent paper (Morris, 1956 a) and will not be dwelt on here. Amongst the estrildines, there are few, if any, species which do not show feather erections of some sort during display. The Silverbill is one of the exceptions here. The Star Finch is also unusual in not erecting fully the ventral plumage. It does however, erect its spotted flank feathers to a dramatic extent. Almost all other species show strong erection of the ventral plumage and often also an erection of the rump, back, nape and head feathers. The throat feathers are typically sleeked, an exception here being the Spice Finch.

The dancing movements of inverted curtseying and pivoting are almost certainly ritualised intention or ambivalent movements. The pivoting seems to be the result of a conflict between fleeing (turning away from the female) and approaching (turning back towards the female). The rhythmic alteration of these two movements produces the stylised dance pattern. The vertical movements of the inverted curtsey dancing are certainly intention movements of jumping upwards and probably derive from intention movements of mounting the female.

The special movements seen in the Zebra Finch and Long-tailed Grassfinch, when pairing, have been discussed fully earlier, and clearly derive from sun-bathing actions.

From this very brief summary of the various display patterns and their origins, it will be seen that a great number of different displays have been built up from a small number of non-signal sources. Furthermore, motivational differences involved in the courtships of different species (typically more fear, or more aggression) give rise to even more variations without using new sources. These further variations take the form of sequential and threshold differences, which give rise to distinctive specific combinations of elements.

DISCUSSION

Despite the large number of facts already collected concerning the distribution, morphology, and ethology of the various estrildine species, the study of the evolution of the group is still in a very preliminary state. Although the investigation by the present author is now terminated, the work is being actively continued by others and the evolutionary suggestions put forward here should be considered rather as guides to further research than as definite conclusions. A preliminary study such as the present one, involving so many species, can only hope to act as a focusing device, bring attention to bear on the more important evolutionary trends and the more valuable species for study. This much can certainly be done here, and, in certain particular instances, specific revisions in the existing taxonomic scheme can be strongly recommended.

As has already been mentioned at various points, the evolution of the group can be thought of as involving either one or two basic invasions of Australia from Africa, via Asia. Either, ancestoral mannikin forms alone spread from Africa, through Asia, to Australia, where they gave rise to all the

grassfinches or, alternatively, both ancestoral mannikins and waxbills spread in this way and each gave rise to part of the Australian grassfinch group. There are facts which support both hypotheses, as we shall see below.

Starting in Africa (but ignoring the waxbills) we have three distinct mannikin types. There are, firstly, the Cutthroat and Red-headed Finches. These birds stand apart from all other estrildines and almost warrant separation into a tribe of their own. Delacour places them with the mannikins, Butler with the grassfinches. Geographical and other considerations make them the most unlikely of grassfinches, however, and Butler is certainly wrong here. Delacour has had to make special allowances for them when including them in his mannikin tribe, but within his rather rigid estrildine framework, he is probably as near the truth as possible.

The Silverbills produce a similar problem. Once again Delacour and Butler disagree, and in exactly the same way. Delacour gives these birds a subgenus to themselves in his mannikin tribe, but Butler sees them as grassfinches. It is true that they have certain similarities to the Australian Cherry Finch and Star Finch, but the geographical distribution of these species is such as to make it unlikely that there is any really close affinity between the three.

The third group to be considered in Africa comprises the Bronze Mannikin, the Black-breasted Mannikin and the Magpie Mannikin. The last of these three is only tentatively included here, as its behaviour is unknown. However, its markings are so similar as to justify placing it here. These three are considered as mannikins by both Delacour and Butler, but Delacour does not even distinguish them subgenerically from species such as the Striated Finch and the Spice Finch. There are sufficient geographical, morphological and ethological differences to warrant at least a subgeneric distinction here.

Moving over to the Asiatic region, the above mentioned Striated Finch and Spice Finch are closely related and should be placed together in the same subgenus. The Spice Finch is slightly closer to the next group, which includes the Chestnut Mannikin, the Pale-headed Mannikin and the Chestnut-breasted Mannikin. A superficially aberrant offshoot from this group is the Java Sparrow. The importance of its unusual morphoplogy dwindles in the face of its behavioural similarities to the more typical mannikin forms. The Pectoral Finch is also very close to this group, being very similar in its markings and colours to the Chestnut-breasted Mannikin. If its sexual patterns include song postures and movements similar to those of the Chestnut-breasted Mannikin, then there will be no need to give this species a subgenus to itself, as Delacour has done.

Passing on to Australia, we find several species of grassfinch with mannikin characteristics. The Long-tailed, Masked, Parson Finch group, with its low voice and lined mouth markings could easily have evolved from a mannikin ancestor. Closely related to these are the Bicheno Finch and Zebra Finch and here again we find a disagreement between previous taxonomic systems. Delacour places the Zebra Finch and Bicheno Finch in a subgenus with the Crimson Finch, Star Finch and Cherry Finch. This is perhaps his unhappiest grouping of all. I prefer to follow Gordon over this point and place the Zebra, Bicheno, Long-tailed, Masked and Parson Finch together in one group, keeping

the others mentioned above separate. I would also like to separate the Gouldian Finch into a distinct subgenus or genus, again following Gordon, but I am equally sure that Delacour is right to relate it to the above species rather than the Parrot finches.

Not having studied the Cherry Finch personally, I can say little about this difficult species except that it is certainly related to the mannikins. It does not appear to have close affinities with any of the other Australian finches, with the dubious exception of the Star Finch.

The Red-browed Finch, the Painted Finch, and the Crimson Finch form a distinct group, closer in character to the waxbills. The Star Finch shows some similarities to this group, but unfortunately it shows some to the Mannikins and the Zebra-Long-tail group as well. So also does the Diamond Sparrow and its close relatives the Fire-tailed and Red-eared Fire-tailed Finches. These birds lie in an intermediate position taxonomically between the waxbill-like Red-browed Finch group and the mannikin-like Long-tailed Grassfinch group. They add considerable support to the theory that the Australian grassfinches are a single (and not a double) natural group. Against this, one has to balance the remarkable similarity between the behaviour of the African waxbills and the Red-browed Finch. The Avadavats exist in Asia as a reminder that waxbill ancestors may have passed this way, and the absence of a nice series of linking forms through from Africa to East Australia, of the kind shown by the mannikins, does not necessarily mean very much. However, on the whole I am inclined to support the single, rather than the double-trend view, after taking into consideration all the known facts, and I am basing my revision of the arrangement of the group, given below, on this. I cannot stress too strongly, however, the tentativeness of this revision. There are so many gaps in our knowledge, that it will probably not be long before a further revision is required, but some of the alterations I am making here will, I hope, stimulate new lines of thought about the evolution of these birds. We badly need to know more about the behaviour of the Avadavats, and the close relatives of the Red-browed Finch, such as the Painted Finch and Crimson Finch. These, in particular, will help to solve the Australian " invasion " problem.

Before presenting my re-arrangement of the species, there are one or two points to be made concerning the validity of the three tribes of the Estrildinae. Delacour has given a number of characters in his paper which define these tribes, and a few modifications are needed here. Firstly, the mouth markings: as already pointed out, these do not follow his groupings perfectly, five species of grassfinch have mannikin-type lines instead of spots. Secondly the voice varies with genus or subgenus rather than with tribe, there being high-pitched mannikins and grassfinches as well as low-pitched ones. Thirdly, both waxbills and grassfinches may sing with the beak pointing upwards. Some grassfinches point it up, others down and others keep it horizontal. Some mannikins keep it down, others keep it horizontal. Fourthly, members of all three tribes are know which hold straws when displaying and this character appears to show a much more scattered distribution through the estrildines than Delacour suggests. Fifthly, the curtsey and pivoting dance movements appear also in species in all three tribes and no general tribal distinctions can be made here.

In other words there are few, if any, "ideal" characters which split the estrildines neatly up into the three tribes suggested by Delacour. Despite all this I am certain that Delacour's *tribal* separation of the species (with the single exception of the Red-browed Finch) is correct in almost all respects. This is, of course, because one includes *many complex character-relationships* in any taxonomic evaluation. Intuitively one is on guard against the ruthless use of single characters, but unfortunately their employment makes for a very tidy report. Delacour's brilliant revision of the 108 estrildine species succeeds in general, I feel sure, not because of the official reasons he gives, but despite them.

CONCLUSION

In concluding, I wish to put forward the following extremely tentative revision of the estrildines. I am including only the species I have discussed in the present paper, and the waxbills are entirely omitted :

1. Genus *Amadina*
   - Cutthroat Finch.
   - Red-headed Finch.
2. Genus *Lonchura*
   - a. Subgenus *Spermestes*
     - Bronze Mannikin.
     - Black-breasted Mannikin.
     - Magpie Mannikin.
   - b. Subgenus *Euodice*
     - Silverbill.
     - Gray-headed Silverbill.
   - c. Subgenus *Lonchura*
     - Striated Finch.
     - Spice Finch.
   - d. Subgenus *Munia*
     - Chestnut Mannikin.
     - Pale-headed Mannikin.
     - Chestnut-breasted Mannikin.
     - Pectoral Finch.
3. Genus *Padda*
   - Java Sparrow.
   - Timor Sparrow.
4. Genus *Aidemosyne*
   - Cherry Finch.
5. Genus *Poephila*
   - a. Subgenus *Poephila*
     - Parson Finch.
     - Long-tailed Grassfinch.
     - Masked Grassfinch.
     - Bicheno Finch.
     - Zebra Finch.
   - b. Subgenus *Gouldaeornis*
     - Gouldian Finch.

6. Genus *Bathilda* — Star Finch.

7. Genus *Zonaeginthus*
   a. Subgenus *Zonaeginthus*
      - Fire-tailed Finch.
      - Red-eared Fire-tail Finch.
      - Diamond Sparrow.

   b. Subgenus *Aegintha*
      - Red-browed Finch.
      - Painted Finch.
      - Crimson Finch.

8. Genus *Erythrura* — Parrot Finches.

In the above scheme, the Cherry Finch and Star Finch are the least satisfactorily placed species. I have only separated them into distinct genera here because at present it is impossible to decide whether to place them with the *Peophila* group or the *Zonaeginthus* group. (Delacour puts them with the former, Gordon with the latter.)

SUMMARY

The behaviour of twenty-seven species of estrildine finches is concisely reported. Brief information is also given about the geographical distribution and the comparative morphology of the Estrildinae. Ethological, geographical and morphological data are then combined in a discussion of the evolution of the group, and finally some minor taxonomic revisions are suggested.

Most of the ethological research has been concentrated on similarities and differences in sexual patterns, and the pre-copulatory behaviour of the following species is described: *Zonaeginthus pictus* (Painted Finch); *Z. bellus* (Fire-tail Finch); *Z. guttatus* (Diamond Sparrow); *Poephila phaeton* (Crimson Finch); *P. ruficauda* (Star Finch); *P. guttata* (Zebra Finch); *P. bichenovi* (Bicheno Finch); *P. modesta* (Cherry Finch); *P. cincta* (Parson Finch); *P. acuticauda* (Long-tailed Grassfinch); *P. personata* (Masked Grassfinch); *P. gouldiae* (Gouldian Finch); *Erythrura* spp. (Parrot Finches); *Padda oryzivora* (Java Sparrow); *Amadina fasciata* (Cutthroat Finch); *A. erythrocephala* (Red-headed Finch); *Lonchura pectoralis* (Pectoral Finch); *L. malabarica* (Silverbill); *L. bicolor* (Black-breasted Mannikin); *L. cucullata* (Bronze Mannikin); *L. striata* (Striated Finch); *L. punctulata* (Spice Finch); *L. ferruginosa* (Chestnut Mannikin); *L. maja* (Pale-headed Mannikin); *L. castaneothorax* (Chestnut-breasted Mannikin); *Estrilda temporalis* (Red-browed Finch).

Many of the sexual displays have been derived from nesting patterns, as a result of the intimate association in time of high intensity reproductive nest-building and high intensity courting. Straw-holding, bowing-with-straw, looping straw, mandibulating, tongueing, and cavity-scooping have been incorporated in the courtship sequences of many species and there are interesting specific differences in the ways in which these patterns have become modified as signals (i.e. ritualised). Displacement beak-wiping is also an important source of ritualised signals in various species; here too there are specific

differences in the extent and nature of the ritualisation. The vertical inverted curtsey dance and the horizontal pivoting dance of the males are derived from intention movements of approaching and avoiding the female. Certain pair-formation ceremonies are shown to be related to sunbathing patterns.

The evolution of the group appears to have taken one of the following two possible courses : The group seems to have originated in Africa and from there to have spread around the Old World to Australia via Asia. This probably involved ancestoral mannikin forms, which gave rise to the grassfinches when they reached Australia. Many of the grassfinches are now extremely convergent with certain African waxbills. The alternative evolutionary scheme, which cannot be ruled out on the present evidence, is that both ancestoral mannikins and waxbills spread round to Australia and that the grassfinch group is not a natural unit, but that part of it has come from ancestoral mannikin stock and part from ancestoral waxbill stock. The former view is favoured here, but it is stressed that more information is required to be certain on this point.

In conclusion, a taxonomic revision is presented, as far as the species discussed here are concerned. This involves the following changes to Delacour's (1943) arrangement : the setting up of three more subgenera (*Spermestes* ; *Gouldaeornis* ; *Aegintha*) and two more genera (*Aidemosyne* ; *Bathilda*) ; the shifting of the Red-browed Finch from the waxbill tribe to the grassfinch tribe, and several other minor alterations. No new names are introduced ; in each case an old name discarded by Delacour has been revived. Delacour's revision of the group was extremely valuable in sweeping away a mass of unnecessary " splitting ", but it over-compensated, and it is now necessary to reverse a few of his more extreme " lumpings ".

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EXPLANATION OF PLATES

PLATE 1

Fig. 1.—Beak-fencing in the Long-tailed Grassfinch.
„ 2.—Ditto ; the left-hand bird uses its far wing in an attempt to regain balance.
„ 3.—Left : The resting posture of the male Star Finch. Right : The singing posture of the male Star Finch.
„ 4.—Low intensity courtship posture of male Zebra Finch (right-hand bird). Note fluffing out of spotted flank feathers.

PLATE 2

Fig. 5.—Zebra Finch—low intensity sunbathing posture.
„ 6.—Longtailed Grassfinch—Bird on right is in wings-drooped pairing posture.
„ 7.—Courtship posture of male Silverbill (on the right). Note the absence of ventral fluffing and also the twisting of the tail towards the female.
„ 8.—Ditto—Showing the arching of the stretched neck.

PLATE 3

Fig. 9.—Semi-low-twist posture of courting male Striated Finch (on left).
„ 10.—Full-low-twist posture of courting male Striated Finch (on right). The female here is a Bengalese Finch. The latter is a pied mutant of the Striated Finch.
„ 11.—Male Striated Finch (on right)—high intensity courtship singing posture, showing crown, nape and ventral ruffling.
„ 12.—Ditto : here the male has pivoted away from the female, by comparing this and the above picture, the pivoting dance movement can be visualised.

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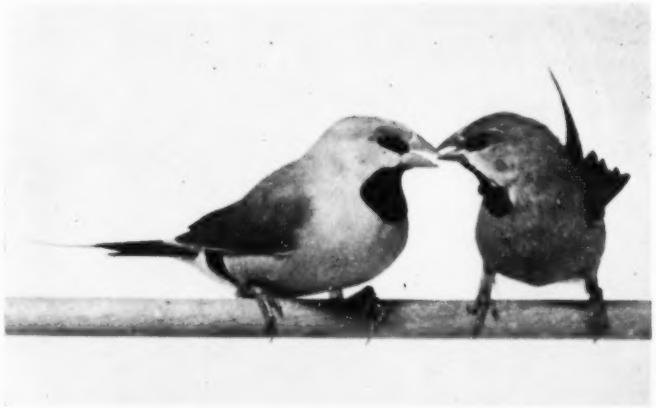

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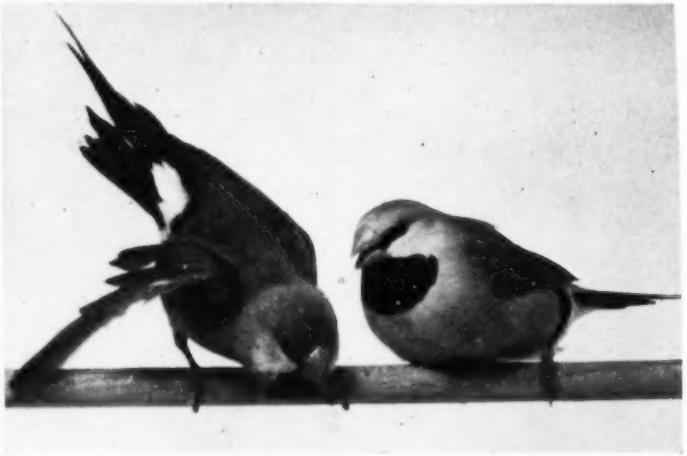

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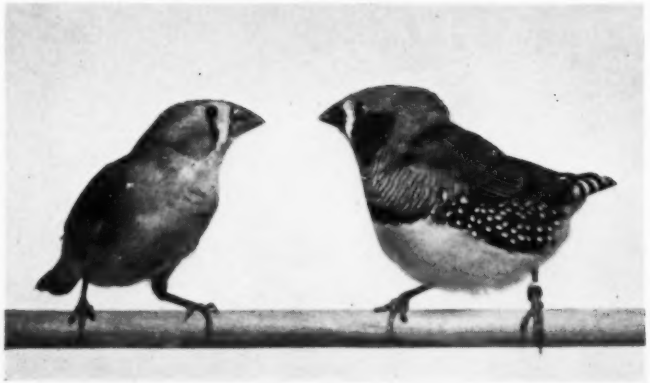

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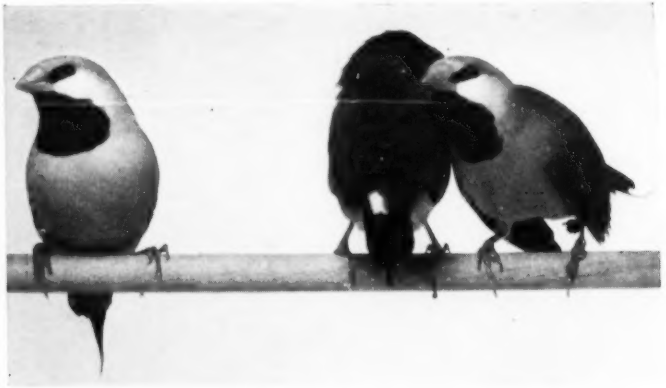

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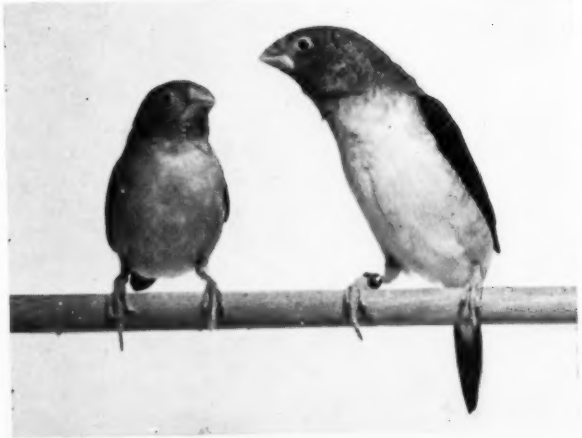

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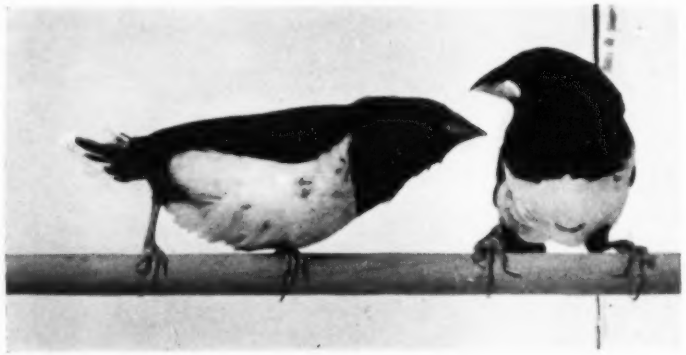

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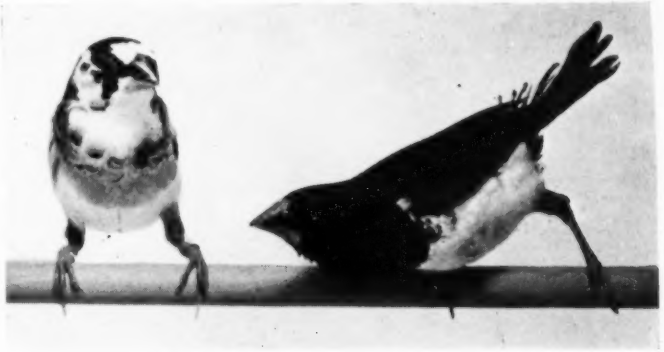

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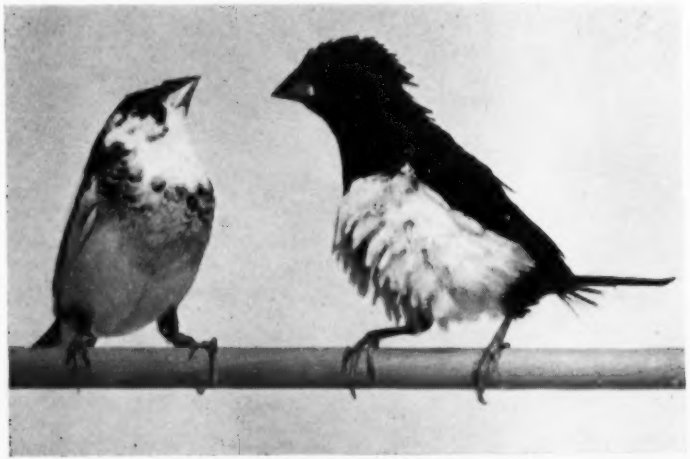

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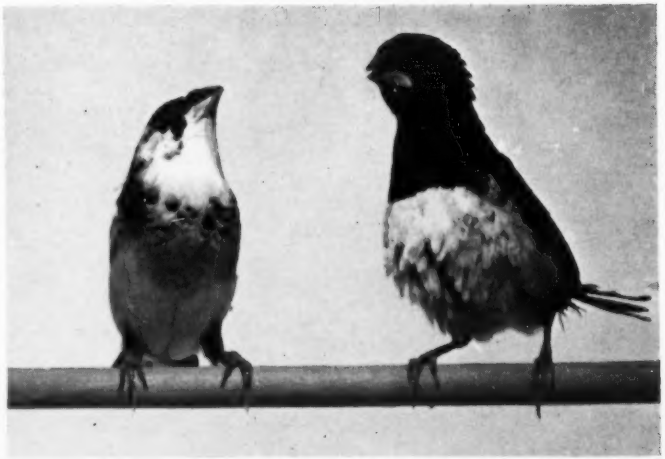

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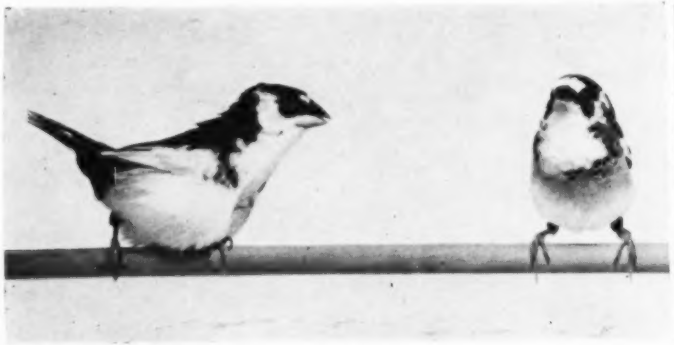

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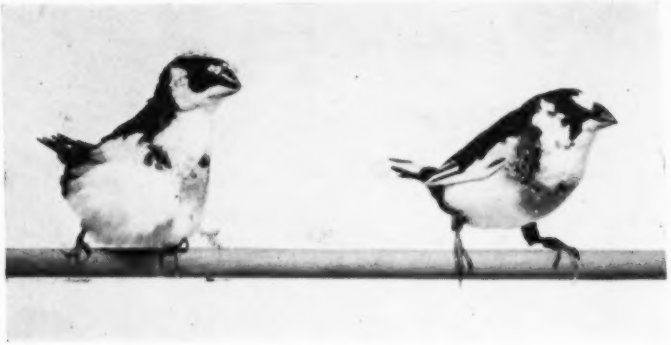

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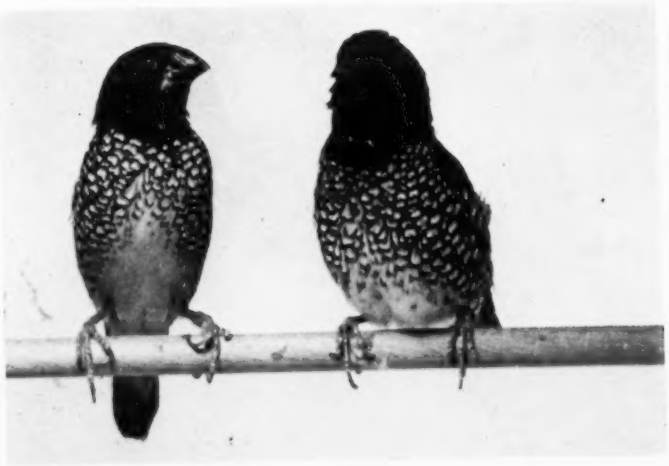

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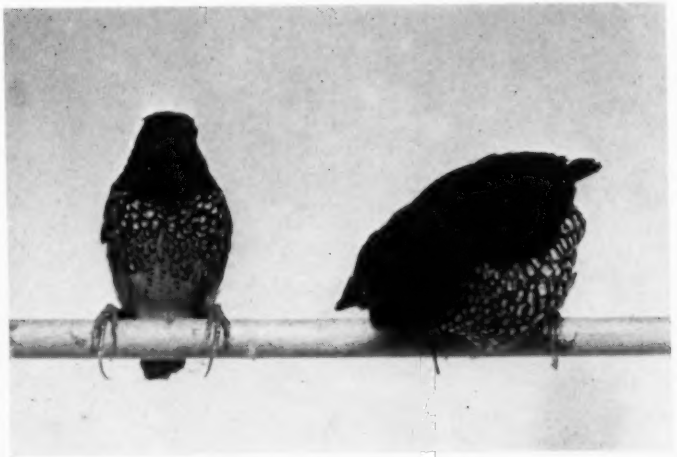

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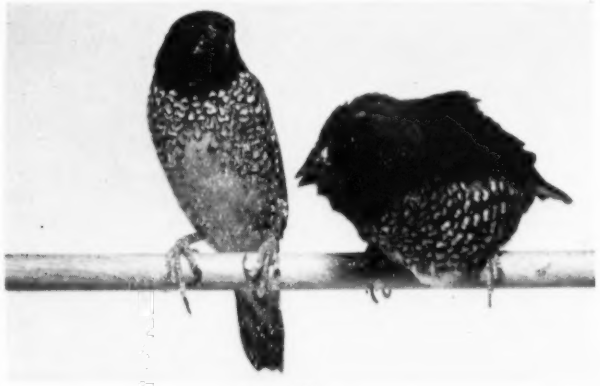

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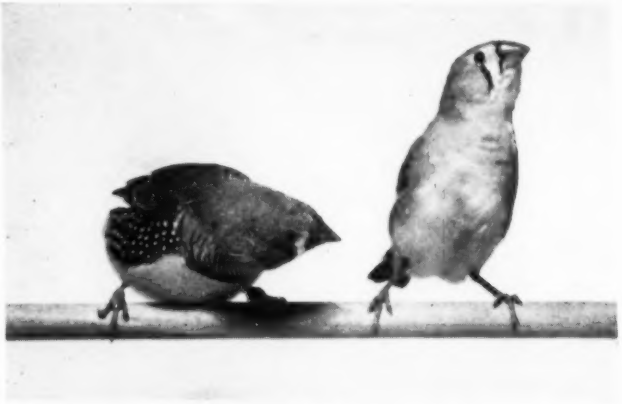

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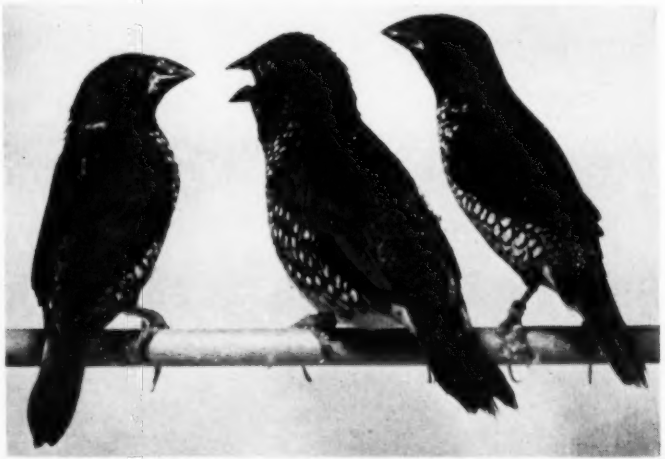

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The comparative ethology of grassfinches and mannikins

PLATE 4

Fig. 13.—Male Bengalese Finch (on left)—medium intensity courtship singing posture.

„ 14.—Ditto : here the male has pivoted away from the female ; cf Fig. 13.

„ 15.—Courtship singing posture of the male Spice Finch. Note the erected head (and ventral) plumage.

„ 16.—Full low twist posture of courting male Spice Finch. Unlike the Striated Finch, the male here sings in this posture and maintains the plumage erection.

PLATE 5

Fig. 17.—Medium low twist posture of Spice Finch (cf. with Fig. 18).

„ 18.—Displacement beak-wiping in the Zebra Finch. The male (left) has been caught in the act of making this quick movement by the electronic flash. A comparison of this with the above suggests that the low twist is a sustained version of displacement beak-wiping.

„ 19.—Peering in the Spice Finch. The (central) singing male is being peered at by two other birds. Note the plumage erection of the singer which contrasts with the sleekness of the peerers.

„ 20.—High intensity peering in the Spice Finch. The singer (left) leans away as the peerer presses close. The full significance of this pattern is not known, but it often has the effect of stopping the singing.

STUDIES OF THE BRAIN, SENSE ORGANS AND LIGHT SENSITIVITY OF A BLIND CAVE FISH (*TYPHLOGARRA WIDDOWSONI*) FROM IRAQ

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(With 1 plate and 4 figures in the text)

CONTENTS

	Page
Introduction	441
The brain and sense organs	442
The brain	442
The eyes	444
Olfactory organs	445
Taste-bud system	445
Lateral line system	446
The ears	446
Comparison of *Typhlogarra* with other blind teleosts	446
Remarks on the behaviour of *Typhlogarra* in aquaria	448
Light sensitivity of *Typhlogarra*	449
Apparatus	449
Procedure	450
Results	450
Discussion	453
Summary	455
References	455
Explanation of plate	456

INTRODUCTION

During the exploration of a labyrinthine pothole system near Haditha in Iraq, Mr A. G. Widdowson and some of his colleagues from the Iraq Petroleum Company found some small blind cyprinid fishes in a subterranean stream (Widdowson, 1954). Mr Widdowson collected some of these fishes and kept them alive for a period of seven months. Later, more of these fishes were discovered in a cave some six miles to the north of Haditha, the position of the cave being close to the Euphrates (latitude 34° 4′N, longitude 42° 24′E). Two fishes were collected and sent to Professor Sir A. C. Hardy who forwarded them to the British Museum (Natural History). They proved to be a new

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species of cyprinid related to the genus *Garra* and they have recently been described by Trewavas (1955) under the name *Typhlogarra widdowsoni*.

At the request of Professor Hardy and the first author, living individuals of this fish were collected (by Mr K. W. Parris). Three of these were sent to Oxford and three kept at the Natural History Museum (from July, 1953). After about a year, one of these latter fishes died and it was taken to prepare a series of transverse sections of the head region. These have been used in our descriptions of the fine structure of the brain and sense organs. Our experiments on the light sensitivity were made on the two remaining individuals.

The second author (Thines 1953, 1954) had already investigated the light sensitivity of the blind cyprinid, *Caecobarbus geertsi* Boulenger, from the Belgian Congo and had compared its reactions with those of the blind Mexican characin, *Anoptichthys jordani* Hubbs and Innes. The apparatus and techniques used in these experiments have been repeated in our work on *Typhlogarra*. In particular we have been interested in comparing and contrasting the behaviour of the Iraq cyprinid with that from the Belgian Congo.

THE BRAIN AND SENSE ORGANS

The brain

The general form of the brain of a *Typhlogarra* may be seen in Fig. 1 together with the brain of a *Garra rufa*, the nearest related species. Comparisons will be made between these two individuals.

The forebrain of *Typhlogarra* is well developed, being relatively larger than that of *Garra rufa*. (The length and breadth of each half of the forebrain in an individual of the former of standard length 42·5 mm. are 1·8 and 1·0 mm. respectively, while the brain measures 5·0 mm. from the tip of the forebrain to the end of the facial lobe. The corresponding measurements in a 51·5 mm. *Garra rufa* are 2·0 and 1·2 mm. in a brain measuring 6·2 mm.). As in most cyprinid fishes, the olfactory bulbs of *Typhlogarra* are close to the nasal sacs, and in the sections nerve fibres can be seen leaving the bulbs and entering the olfactory lamellae. The microscopic structure of the forebrain is much like that described for other teleosts by Kappers (1934) and by Kappers, Huber & Crosby (1937). Since the forebrain of teleosts is largely concerned in olfaction (Prosser *et al.* 1950), and as the olfactory organs are normally developed, (see page 445) there is every structural indication that the olfactory sense of *Typhlogarra* is in no way degenerate.

But the optic lobes, as Trewavas (1955) has seen, are much regressed. The lobes do not meet in the middle line of the brain, nor do they extend over the valvulae of the cerebellum. Compared with *Garra rufa*, having optic lobes 2·0 mm. in length and 1·5 mm. in breadth, the corresponding dimensions in *Typhlogarra* are 0·4 and 1·0 mm.

The microphotograph (Plate 1) shows that only the lateral parts of the optic tectum remain. In a normal teleost brain there is a thickening of the tectum (*torus semicircularis*) at the region of junction with the underlying tegmental parts of the brain, but no such thickening is evident in the sections

of *Typhlogarra*. However, vestiges of the tori longitudinales can be found, these being two slightly thickened areas on either side of the midline.

The fine structure of the remnants of the optic tectum is not readily comparable with that of a teleost with normal vision. Kappers, Huber & Crosby (1937) recognize six strata in the optic tectum: (1) an outer layer of optic tract fibres followed by; (2) a stratum of alternate layers of nerve fibres and cells; (3) a central " grey " stratum; (4) a central " white " stratum; (5) a periventricular " grey " stratum; and lastly (6), a periventricular fibre stratum. In *Typhlogarra* there are remnants of an outer fibre layer and this is followed by two sparse layers and a thick " grey " layer, which are presumably the remains of strata 2 and 3. Nothing appears in the sections corresponding with stratum (4), but there is a periventricular layer of nuclei, which are shown in the more median cuts through the optic lobes.

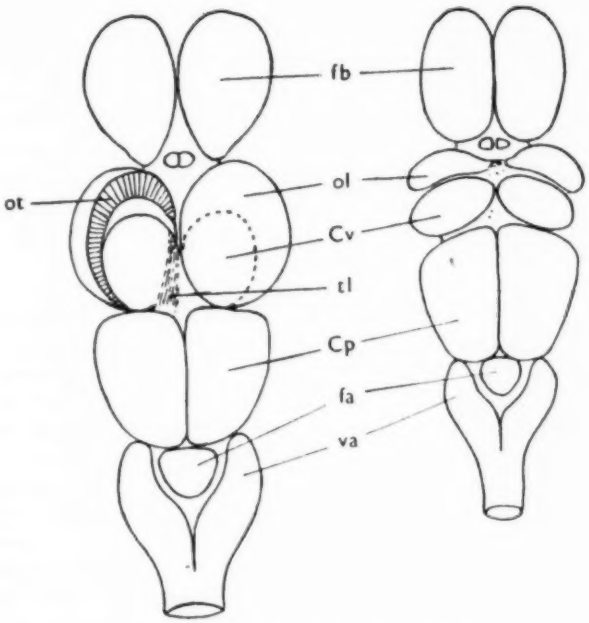

Fig. 1.—The brains of *Garra rufa* (on the left) and *Typhlogarra widdowsoni*, as seen from above. (×20) fb, forebrain; ol, optic lobe; ot, optic tectum; cv, valvulus of cerebellus; cp, posterior part of cerebellum; tl, torus longitudinalis; fa, facial lobe; va, vagal lobe. (The longitudinal furrow down the posterier part of the cerebellum is not found in all individuals.)

Comparisons of the cerebella of the two species reveals that the valvulae are better developed in *Garra rufa* than in *Typhlogarra* (see Fig. 1), a difference that is perhaps related to the regression of the optic lobes in the latter. But little seems to be known of the functions of the valvulae (Dow, 1942).

There are no marked differences between *Typhlogarra* and *Garra rufa* in the relative development of the facial and vagal lobes of the hind brain.

Compared with other cyprinid fishes (Evans 1931) the facial lobes of *Typhlogarra* are not so large as in the barbel (*Barbus barbus*), gudgeon (*Gobio gobio*) or loach (*Nemachilus barbatulus*), rudd (*Scardinius erythrophthalmus*), chub (*Leuciscus cephalus*) and dace (*Leuciscus leuciscus*). Furthermore, the vagal lobes of *Typhlogarra* are not so relatively small as in these latter four species, nor are they so strongly developed as in the carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), bream (*Abramis brama*) and tench (*Tinca tinca*).

Herrick (1903) and Dijkgraaf (1933) have shown that in siluroid and cyprinoid fishes the taste buds of the outer skin are supplied by branches of the facial nerve and that a marked accentuation of the facial lobe is correlated with an extensive proliferation of taste buds in the skin of the head, body and fins. Taste buds within the mouth are connected with fibres of the glossopharyngeal and vagus nerves. Some cyprinid fishes have a palatal organ in the roof of the pharynx consisting of comb-like ridges of the mucous membrane abundantly supplied with taste buds. Such an elaborate taste receptor system is presumably correlated with unusually large vagal lobes. In *Typhlogarra* there is no palatal organ, although the roof and floor of the mouth are dotted with taste buds. And the taste buds in the outer skin are confined to the head (see Fig. 2), not spread over the body and fins as in some cyprinids. So in *Typhlogarra*, moderate extensions of the inner and outer taste receptors would seem to be reflected in moderate developments of the two associated brain centres.

The eyes

The eyes of *Typhlogarra* are very regressed. Externally, no trace of the eyes can be seen, even under a binocular microscope. At each side of the head on a level with the olfactory organ is a small pit around which curves the suborbital branch of the lateral line system. But this pit is not so prominent in two of the specimens mainly on account of the padding out of the skin through extensive subcutaneous deposits of fat.

The microphotograph (Plate 1) shows the eyes in a cross section of the head. It will be seen that the eyes are withdrawn into the head close to the bones surrounding the forebrain. The individual used for the head sections was 30·5 mm. in standard length and the width of the right eye (excluding the vestiges of the anterior chamber) is about 0·25 mm. In both eyes the sclerotic cartilages are well developed and practically enclose the posterior chambers. There is an opening for the exit of the remnants of the optic nerve, which soon ends blindly after emerging from the capsules.

Without a developmental series the interpretation of the homologies of the eye parts is not easy. However, the right eye more readily lends itself to such consideration. Figure 3 shows that the posterior chamber is almost enclosed in sclerotic cartilage, except where there is a connection with the remains of the anterior chamber. Certain rounded groups of cells in this part are most probably regressed lens tissues. Attached to the walls of the sclerotic capsule is a substantial layer of large connective tissue cells, presumably being regressed sclerotic and choroidal tissues. This layer extends around an inner sac which must represent the relics of the retina. Large columnar cells extending over

the inward walls of the retinal sac may represent the pigment layer, which is immediately followed by a zone of diffuse tissues with numerous relatively large, medium-dark staining nuclei. At the outward side of the sac is a group of numerous, smaller, dark-staining nuclei. Perhaps these latter are the ganglion cells, while the larger nuclei are the remnants of the nuclear and reticular layers.

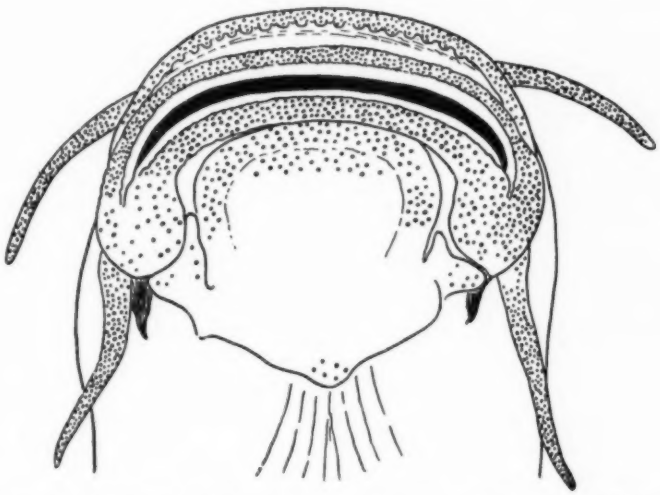

Fig. 2.—The underside of the head of *Typhlogarra widdowsoni* ($\times 60$). The black dots represent the taste buds.

Olfactory organs

Compared with *Garra rufa*, its nearest relative, *Typhlogarra* has olfactory organs of much the same level of development. A *Typhlogarra*, 42 mm. in standard length, has the head 12 mm. in length, while the chamber bearing the olfactory lamellae measures 2·0 mm. in length and 1·2 mm. in breadth. The central rachis bears 22 well formed lamellae. A *Garra rufa* of standard length 51·5 mm. with a head 12 mm. in length has olfactory chambers, each about $2{\cdot}0 \times 1{\cdot}3$ mm. containing some 20 olfactory lamellae.

Taste-bud system

As already mentioned, the outer taste buds are confined to the head. Figure 2 shows the distribution of the taste buds on the under surface of the head, and it will be noticed that the buds are densest on the barbels and lips. In these regions there are about 16 to 20 taste buds per mm., that is about 250 to 400 per square mm. These sense organs are also very numerous over the front part of the snout, between the upper lip and a line joining the two anterior nostrils. Over the lower parts of the cheeks and gill covers and over the interorbital region the taste buds are quite sparse.

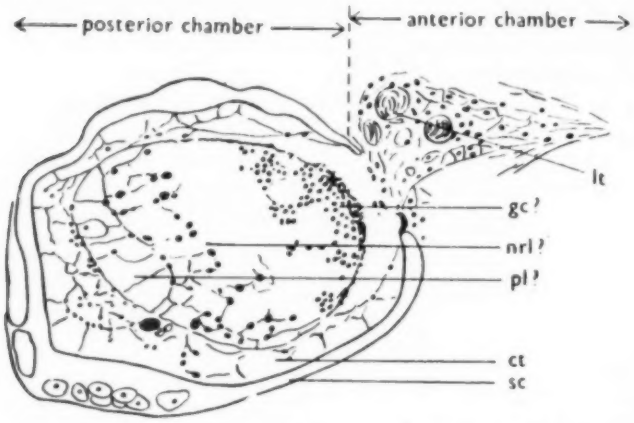

Fig. 3.—The regressed right eye of *Typhlogarra widdowsoni* (×450). sc, sclerotic cartilage; ct, regressed connective tissues (remains of sclerotic and choroidal tissues); lt, regressed lens tissue; gc? ganglion cells; nrl? nuclear and reticular layers; pl? pigment layer.

Lateral line system

The canal system of *Typhlogarra* conforms to the pattern found in cyprinid fishes (Tretiakov, 1944.) In the head sections neuromast organs can be seen in the canals, and in general the lateral line system seems much like that in *Garra rufa*. It is certainly not highly developed.

The ears

The inner ears of *Typhlogarra* are in no essential way different from those of other cyprinid fishes.

COMPARISON OF *TYPHLOGARRA* WITH OTHER BLIND TELEOSTS

In certain blind fishes, for instance *Anoptichthys jordani* and *Caecobarbus geertsi*, the eyes are normal in form in the young stages but regress as the fish becomes adult. (Luling (1955)), Quaghebeur (1957). Comparison of a single individual of *Typhlogarra* with such better investigated blind fishes must therefore be limited in scope, so far as the eyes and optic centres are concerned. However, the *Typhlogarra* that was sectioned was 30·5 mm. in standard length while the largest specimen in the collections is 46 mm. This fact and the general features of structure show that the sectioned fish was fully adult. And, as will be seen, the degree of regression of the eyes and optic lobes of our specimen is certainly not less than that of adult *Caecobarbus* and *Anoptichthys*. It is reasonable, then, to make comparisons at the adult level.

There is, however, another possibility. In adult fishes of a particular size range, there may be some variation in the degree of regression of the eyes and optic lobes. It is with these limitations in mind that the following brief account is given.

Ramsey (1909) and Charlton (1933) have studied the gross and fine structures of the optic lobes of various cave-dwelling amblyopsid fishes, the former working on *Amblyopsis spelaeus* and the latter on *Troglichthys rosae* and *Typhlichthys eigenmanni*. The optic lobes are much regressed, this being particularly true of the dorsal regions. In *Amblyopsis* Ramsey (1909) remarks that " . . . the torus longitudinalis, which in the normal brain is suspended in the ventricle in the median line entirely below the layers of the lobes, is *between* the lobes and on nearly the same level with them ". Conditions in the other two amblyopsid genera are rather similar. However, both workers were able to trace most of the cell layers in the better developed, lateral parts of the optic lobes. (In *Amblyopsis* the optic fibre layer (2) is absent while layers 4, 5 and 6 (see page 443) are reduced).

More recently, Stefanelli (1954) has used the characin *Anoptichthys jordani* for studying the differentiation of the neurons in the optic lobes of a blind fish. In comparing the optic lobes of this species with related species having fully developed eyes (*Astyanax mexicanus* and *Pristella riddlei*), he found that the dorsal parts and the torus semicircularis were particularly regressed. Of the optic cell layers, the superficial layer is absent, while layers 2 and 3 (see page 443) are reduced in thickness.

Quaghebeur (1957), who worked on *Caecobarbus geertsi*, finds that the dorsal parts of the optic lobes are very much reduced in the adults, although the tori longitudinales can be clearly seen. Concerning the layers of the optic tectum, he observed that the layers are all developed except one, the superficial stratum opticum, which is either absent or much reduced. Layer 2 (stratum fibrosum) is reduced in thickness.

To summarise, these blind fishes have an optic tectum with very reduced dorsal parts, in which the tori longitudinales are on much the same level as the better developed lateral parts. In these latter most of the layers can be recognized but there is some reduction (or loss), notably in the superficial optic fibre layer and in the underlying stratum fibrosum (layer 2). As the optic nerves have little or no connection with the brain in the adult phase, this might have been expected.

Turning now to *Typhlogarra*, the gross structure of the optic tectum is much like that immediately described, but it is even further reduced. It can be regarded as coming at the end of the following morphological series.

1. Teleosts with normally developed eyes: optic lobes curving over to meet in the mid-line of the brain. Tori longitudinales well below the tectum.

2. *Anoptichthys jordani*: optic lobes almost meeting in the mid-line of the brain. Tori longitudinales a little below the level of the tectum.

3. Amblyopsidae and *Caecobarbus*: dorsal parts of the tectum very reduced. Tori on the same level as the lateral tectal parts.

4. *Typhlogarra*: dorsal parts of tectum extremely thin. Tori vestigal.

Finally, the component layers of the optic tectum can hardly be recognized in our specimen of *Typhlogarra* We may conclude that the optic centres of this fish are more regressed than in any other previously investigated blind fish.

REMARKS ON THE BEHAVIOUR OF *TYPHLOGARRA* IN AQUARIA

Like other blind fishes, *Typhlogarra* wanders, seemingly at random, over a confined space, its movements giving the impression that it is steadily carrying out a sensory scanning of its surroundings. As in *Caecobarbus* ". . . on peut l'observer explorant calmement tout l'espace libre de l'aquarium, si ce dernier est de dimensions assez considérables " (Thines 1955). It moves slowly and rather jerkily, the characteristic motion being a series of glides between flicks of the tail. After a single tail flick a fish will " coast " until the momentum dies down and then the tail will flick again, and so on. The interval between tail beats is usually anything from one to ten seconds. From time to time a fish will poise itself in midwater or rest on the bottom, but in general the time spent in motion is considerably more than that spent at rest. As such, *Typhlogarra* (and other blind fishes) readily lend themselves to the type of experiment we carried out on light sensitivity.

When presented with a current, such as is generated by rotating a large circular aquarium with a central cylinder resting on the bottom, *Typhlogarra* immediately turned into it. This quick rheotactic response was made without any tactile reference to the sides of the aquarium, so far as we could see. Certainly no such tactile reference was necessary as Dijkgraaf (1933) found to be essential for response to currents by blinded minnows. At current speeds of five to twenty feet per minute the fish would swim vigorously with the pectoral fins pulled in towards the flanks. But under these conditions the tail was not in continual motion. After a burst of activity there would be a brief pause before the next burst, and as the current slowed down, the number of beats in each burst would be reduced to one or two. When the current speed fell away to about two feet per minute the fish would nearly always turn out of the current and allow itself to gently drift before resuming its still-water mode of swimming.

In the pothole where *Typhlogarra* was first discovered, Mr Widdowson has informed us that the stream ran at about two miles per hour and that the fishes swam in the shallows where the current was not so fast.

Finally, a comparison of some aspects of the behaviour in captivity of *Typhlogarra* and *Caecobarbus* has some relevance to this paper and is particularly interesting in that two blind cyprinid fishes are involved. When two *Typhlogarra* are going to meet neither shows any evasive action but they gently move apart when about to collide. Similarly, when a fish is approaching a wall of the aquarium it only turns away at the last second or after a brief contact with the wall. Evidently, the lateral line sense is not so well developed as in some fishes with normal vision (Dijkgraaf (1952). But a *Caecobarbus* seems to have a better spatial sense of its aquarium (Thines 1955). On approaching an aquarium wall or another individual, it changes direction and suddenly accelerates its swimming rhythm when it is from half to two centimetres away from the obstacle. Or on meeting, one fish may attack the other.

There is also a marked difference in mechanical sense. With *Typhlogarra* even a heavy bang on the aquarium table or a sharp rap on the side of the tank often fails to elicit any detectable reaction. If there is a response it

consists of a sudden but not vigorous " start " by the fish. A slight tap on an aquarium containing *Caecobarbus* leads to a violent reaction and often to the fishes jumping out of the water.

The temperature relations of the two species are also very different. The stream in which *Typhlogarra* was first discovered was clear and warm, around 20°C. But like Mr Widdowson (see Trewavas, 1955) we found that these fishes were tolerant of a wide range of temperature, from about 10° to 20°C. On the other hand, *Caecobarbus* must be kept at a temperature of at least 21°, and preferably at the optimum temperature of 22·5°C. Failure of the temperature control soon leads to death; or if the fishes survive, they become diseased.

It will thus be seen that these two blind cyprinid fishes are very unlike in their behaviour and physiology. In the next section we shall also show that there are marked differences in their light sensitivity.

LIGHT SENSITIVITY OF *TYPHLOGARRA*

Apparatus

The reactions to light of *Typhlogarra* were determined with precisely the same apparatus used in studies of *Caecobarbus geertsi* and *Anoptichthys jordani*, (Thines 1953, 1954). Briefly, there are three successive dark chambers: the first is the dark room itself; the second is made by completely investing a metallic frame with a dark cloth; while the third, which contains the aquarium, consists of a box made of blackened cardboard with a lid containing an opening for the light source. This consists of a 100 watt bulb with incorporated reflector, the light passing through an optical system consisting of a condenser lens and an objective such as is used in enlarging photographs. There is a diaphragm for controlling the amount of light. This light source is air-cooled and it has been shown elsewhere (Thines, 1953) that the water in the tank is not heated during the experiments.

The light source was adjusted so as to throw on the table a luminous rectangle that is just half the total area of the water surface of the aquarium. In order to have a sharp separation between the dark and light halves, a metallic screen was placed vertically in the aquarium, so that its shadow fell exactly on the dividing line. The dark half of the aquarium had a black wooden cover in order to eliminate any possible effects of light. The aquarium was mounted on rubber tubing in order to avoid vibration.

In our experiments " white " light and filtered light were used as follows:—

Achromatic light	(30 lux)
Monochromatic blue filter	(400–700 A°)
Monochromatic green filter	(±5400 A°)
Monochromatic yellow-green	(±550 A°)
Monochromatic yellow	(500 A°+)
Monochromatic orange	(5600 A°+)
Monochromatic red	(6500 A°+)

Procedure

The method simply consists of observing the length of time spent by the fish in the lighted and dark halves of the tank during the experiment. In our experiments the fish was given a " settling-down " period of fifteen minutes before the observations were made. The two fishes were used in alternate experiments lasting fifteen minutes. A small window in the chamber enclosing the tank enabled the observer to record the time spent by a fish in the lighted zone, this being done by a paper-band chronograph. Twenty experiments were carried out for each type of light source, and the positions of the light and dark zones were switched round at every other experiment so as to eliminate any possible effects of learning. No more than four experiments of fifteen minutes in a half-day were carried out, and the fishes were allowed to rest for about an hour between sets of two experiments. Between experiments the fishes were kept in a dark room.

Results

The results are summarised in Tables 1, 2 and 3, the records being expressed as percentage times spent by a fish in the dark half of the aquarium. Table 1 gives the mean percentage for the two fishes during each of the twenty series of experiments. We have also given separate results for each of the two fishes in Tables 2 and 3, these, of course, being calculated from a series of ten experiments.

Considering first the two fishes together, Table 1 shows that there is a general but rather slight preference for the dark part of the aquarium. Excluding the mean for yellow light (49·5), the dark-end percentage figures vary from 57·65 to 61·82. Students " t " test was applied to these, and the values of " t " indicate that all the differences between the means are statistically significant.

Turning now to the results for each fish, Tables 2 and 3 show that Fish No. 1 (Table 2) has a more definite photonegative response (60 per cent) than Fish No. 2 (55 per cent). The standard deviation (σ) as an expression of the individual variability of each fish, shows that Fish No. 2, with a smaller value of σ, is more consistent in behaviour.

Rather strikingly, both fishes showed no photonegative bias when given yellow light as the contrast to darkness. At present we can merely draw attention to these results, which seem well worth further investigation.

We have concluded that *Typhlogarra* displays a slight photonegative response to light, a response that is close to the point of indifference. The similarity of the results for the different coloured lights, which are plotted in Fig. 4, show that *Typhlogarra* is indifferent to wave length. We thus suggest that the phototropisim exhibited is most probably a reaction to the difference in brightness between the two zones of the experimental tank.

Compared with *Typhlogarra*, both *Caecobarbus* and *Anoptichthys jordani* show marked photonegative responses, when presented with light and dark zones under the same experimental conditions. It has already been pointed out (Thines 1954) that the reactions of *Anoptichthys* are less marked but more

TABLE 1

General results on the phototropism of *Typhlogarra widdowsoni*

	Achromatic light	Red light	Blue light	Orange light	Green light	Yellow light	Yellow green light
Mean of 2 specimens (Percentage Darkness)	57·65	59·27	60·71	58·90	61·82	49·56	57·95
Standard deviation (σ)	11·89	18·32	16·21	10·56	13·71	10·54	15·24
"t"	2·80	2·20	2·88	3·48	3·75	0·18	2·27
	Between 1 and 2 experiments in 100 will give a divergence from the mean as large as that actually found	Between 2 and 5 experiments in 100 will give a divergence from the mean as large as that actually found	Less than 1 experiment in 100 will give a divergence from the mean as large as that actually found	Less than 1 experiment in 100 will give a divergence from the mean as large as that actually found	Less than 1 experiment in 100 will give a divergence from the mean as large as that actually found	More than 50 experiments in 100 will give a divergence from the mean as large as that actually found	Between 2 and 5 experiments in 100 will give a divergence from the mean as large as that actually found

TABLE 2

Specimen 1. *Typhlogarra widdowsoni*

	Achromatic light	Yellow green light	Yellow light	Green light	Orange light	Blue light	Red light
Means of specimen No. 1 (percentage darkness for 10 times 15 min.)	55·14	60·36	48·50	65·07	60·65	67·56	66·10
Standard deviation; (σ)	5·20	8·57	8·62	12·71	10·88	15·19	16·68
"t"	2·97	3·62	0·52	3·55	2·93	3·47	2·90

General mean of specimen: 60·48; (σ) = 6·27

TABLE 3

Specimen 2. *Typhlogarra widdowsoni*

	Achromatic light	Yellow green light	Yellow light	Green light	Orange light	Blue light	Red light
Means of specimen No. 2 (Percentage darkness for 10 times 15 min.)	60·17	55·54	50·16	58·56	57·14	53·88	52·53
Standard deviation; (σ)	15·59	19·48	12·12	13·87	9·92	14·15	17·41
"t"	1·96	0·85	0·03	1·85	2·16	0·82	0·44

General mean of specimen: 55·42; (σ) = 3·25

consistent than those of *Caecobarbus*. The means of the percentage times spent in the dark half of the aquarium ranged from 68 to 96 for *Caecobarbus* and 59 to 70 for *Anoptichthys* (Thines 1954). The corresponding figures for *Typhlogarra* (using only two fishes instead of three to six) are 50 to 63 per cent. The reactions of the three fishes thus fall into a series ranging from a marked photonegative to a near-indifferent kind of response.

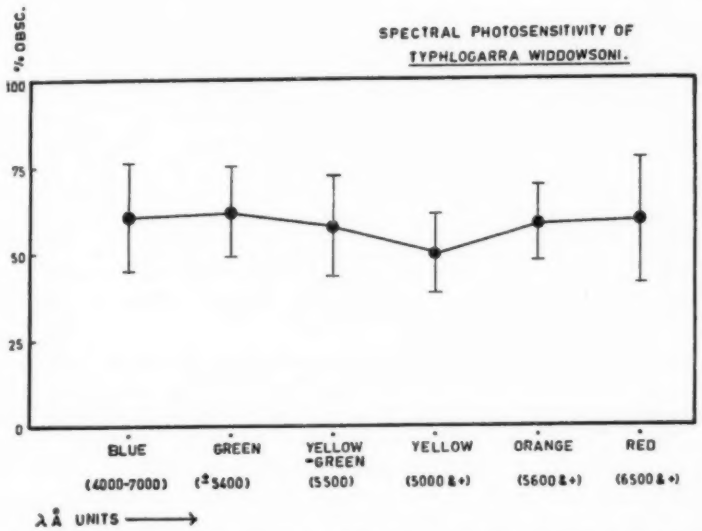

Fig. 4.—Graph showing the spectral sensitivity of *Typhlogarra widdowsoni*. Each point represents the mean of 20 observations of 15 minutes on the two fishes. The vertical line drawn through each point gives an indication of the standard deviation in both positive and negative directions.

Discussion

It is remarkable that these three species of blind fishes should react to differences in brightness. The lack of wave-length discrimination is less surprising, for colour vision presupposes the presence of a functional retina and normally developed dioptic parts of the eye. A number of teleosts can discriminate between colours (Walls, 1942; Herter, 1953) but in the lightless environment of blind fishes this is obviously impossible.

It is clear that the very regressed eyes of *Typhlogarra* can play no part as light receptors if only because the optic nerves make no contact with the brain In *Anoptichthys jordani*, and in other blind characins, Breder & Rasquin (1947) found that: " The phototaxis exhibited, either positive or negative is mediated through the remnant of the optic cyst, since both types become light indifferent on removal of the cysts. However, some fish in all the more advanced population are light indifferent and have no nervous connection between the cyst and the brain ". But adult *Caecobarbus* are markedly photonegative and have very

General mean of specimen: 55·42; (σ) = 3·25

regressed eyes that have no linkage with the brain. In this instance, extraocular light receptors must be involved (Thines 1953, 1954).

Breder & Rasquin (1947 and 1950) have also reviewed the evidence for the rôle of the pineal organ in chromatophore control and light reactions of teleosts and have given an account of their own findings. In the earlier paper they found that fishes with a pineal exposed to light were photopositive while those with this complex masked were photonegative in responses. The later paper is a preliminary account of a general survey, but here again the light-negative fishes (four species) were found to have permanently covered pineal areas, which is also true of a near-indifferent-to-light species, *Cyprinodon baconi*.

The pineal complex of *Typhlogarra* has a structure much like that of other cyprinid fishes. The epiphysis lies immediately under a thin transparent area of the skull—actually under the junction between the two frontal bones. The skin has no pigment cells and is translucent, all of which suggests that the pineal is exposed to light, at least to intensities comparable with those used in our experiments. However, Breder & Rasquin (1950) found that the grey mullet, *Mugil trichodon* has an exposed pineal area and is light-negative. *Typhlogarra*, which would seem to have an exposed pineal, is slightly light negative.

Evidentally the functional theme discovered by Breder & Rasquin (1950) has a number of variations, some of which they have already appreciated. Considering the diversity of the teleosts, they remark that conformity to certain functional schemes is more surprising than the exceptions.

There is the further possibility that cutaneous light receptors may also be involved. The silverside *Membras stipes* was found by Breder & Rasquin (1950) to have an exposed pineal area and to be a photopositive species. After covering the pineal area and blinding the fish, they found it to be still photopositive, but to a lesser degree. Two other species with screened pineal areas, *Eucinostomus gula* and *Haemulon melanurum*, still responded to light after being blinded.

Comparable experiments on blind fishes have yet to be tried. Breder & Rasquin (1947) found that some of the more advanced blind characins from Mexico were light indifferent and had no nervous connection between the eye remnants and the brain. Presumably the fish have no light receptors, whether these be pineal or dermal. As the pineal in these forms is exposed to light, phototaxis seems to depend on interplay between the pineal complex and the eye remnants, provided the latter are coupled to the brain. *Caecobarbus* and *Typhlogarra*, with exposed pineals and no connection between the optic cysts and the brain, are markedly and slightly photonegative respectively. Is the interplay in *Caecobarbus* between cutaneous and pineal receptors? Has *Typhlogarra* nearly lost its cutaneous light sense? These are some of the questions for further experiments.

Clearly there are a number of possible stages in the evolution of blind fishes. Each species will require more study if general problems are to be comprehended. Close ecological studies, when coupled with further experiments, should throw more light on the surprisingly diverse biology of cave fishes.

SUMMARY

1. The structures of the brain and sense organs of *Typhlogarra widdowsoni*, a blind cave fish from Iraq, are described and compared with those of *Garra rufa*, the nearest related species.

2. In *Typhlogarra* the optic lobes and eyes are very regressed. Only the lateral parts of the optic tectum are developed and these incompletely. The optic nerves do not connect with the brain and the different parts of the eye are not easily recognisable.

3. Experiments on the light sensitivity showed that *Typhlogarra* is slightly photonegative, but indifferent to the wave length. It is quite unlike *Caecobarbus geertsi*, a blind cave fish from the Belgian Congo, which is markedly photonegative. Other differences in behaviour are also considered

4. More general comparison of *Typhlogarra* with other blind species re-emphasises that such fishes are remarkably diverse in their biology.

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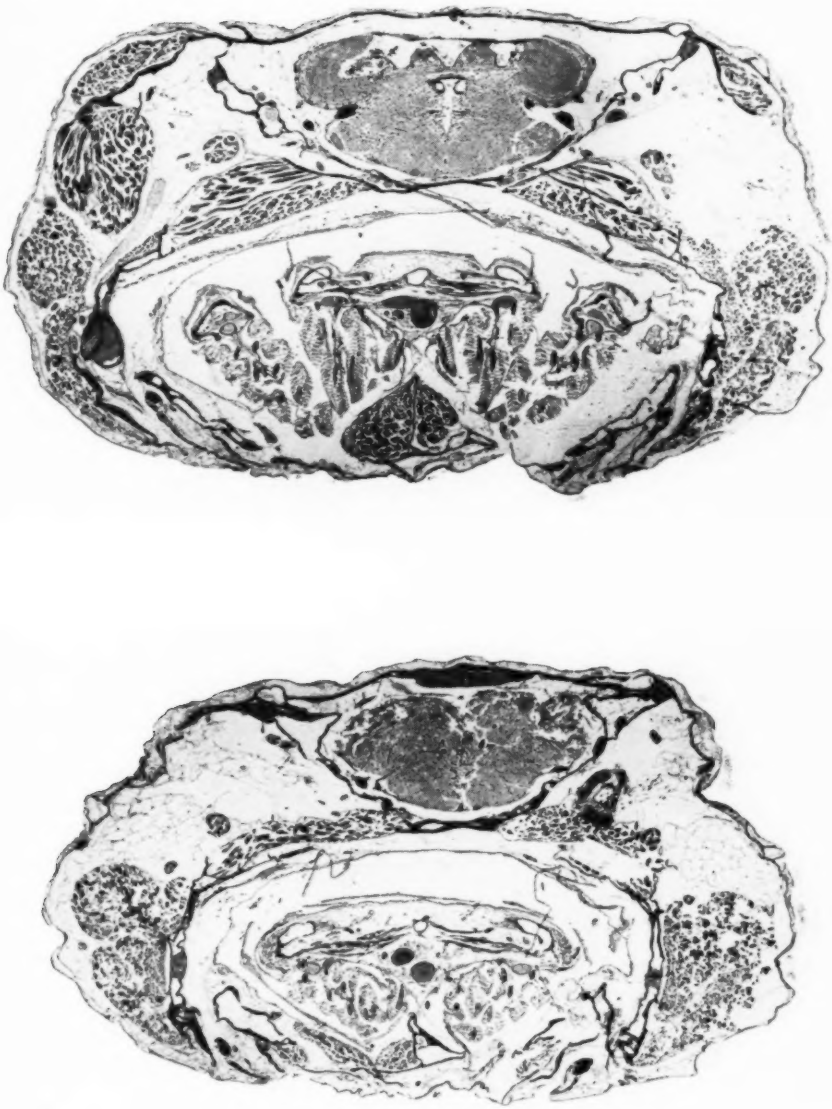
EXPLANATION OF PLATE

Upper microphotograph. Transverse section through the head of a *Typhlogarra* to show the regressed optic lobes of the brain ($\times 30$).

Lower microphotograph. As above, showing the regressed eye on the right, the centre of which is on a level with the lower edge of the brain. The sclerotic cartilage through which passes a very reduced optic nerve, can be seen along the inner side of the eye.



Transverse section through the head of a blind cave fish, *Typhlogarra*

SOME VARIATIONS IN THE MAXILLARY NERVE OF PRIMATES

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(With 2 figures in the text)

CONTENTS

	Page
Introduction	457
Materials and methods	459
Anatomical material	459
Dissection	459
Anatomical nomenclature	460
Results	460
Tree shrew, Lemur, Loris and Galago (Prosimii)	460
Zygomatic nerve	460
Dental nerves	460
Passage through infraorbital canal	460
Facial distribution	462
New World Monkeys (Ceboidea)	462
Zygomatic nerve	462
Dental nerves	463
Passage through infraorbital canal	463
Facial distribution	463
Old World Monkeys (Cercopithecoidea)	464
Zygomatic nerve	464
Dental nerves	464
Passage through infraorbital canal	464
Facial distribution	466
Apes and Man (Hominoidea)	466
Zygomatic nerve	466
Dental nerves	466
Passage through infraorbital canal	467
Facial distribution	467
Discussion	468
Acknowledgments	469
Summary	469
References	470

INTRODUCTION

Classical accounts of primate anatomy have provided considerable information about differences in facial structures associated with the terminal branches of the maxillary nerve. Many of these variations have been summarized in comparative studies (Huber, 1930; Lightoller, 1928, 1934; Pocock, 1914, 1918; Wood Jones, 1929), and it is clear that with few exceptions the most striking

changes in non-skeletal features affect first, the rhinarium and vibrissae, and second, the facial muscles.

In the tree shrew, lemur, loris and galago, a moist, naked rhinarium extends over the entire tip of the snout. There is a well-developed group of mystical vibrissae on the upper lip, while smaller submental and interramal groups are found under the lower jaw, together with genal and supraorbital tufts near the eye. The facial musculature is in these forms relatively uncomplicated, and consists mainly of fibres which move the vibrissae. In *Tarsius*, although the rhinarium is reduced to a narrow band of naked skin around the nostrils, a full set of facial vibrissae is present, and the facial muscles are only a little more differentiated than in other prosimians. In monkeys and apes the rhinarium has disappeared completely, and whereas small groups of mysticial and supraorbital vibrissae are found in many New and Old World monkeys, in the apes they are reduced to inconspicuous sinus hairs. Facial musculature on the other hand, shows a progressive elaboration, and sometimes additional specialized facial structures develop. For instance, in the cercopithecoid monkeys, there are cheek pouches for the temporary storage of food, while in the male orang-utan a fibrous cheek pad often forms a conspicuous facial feature. In man there is neither rhinarium nor vibrissae, but the mimetic musculature is more highly developed than in any lower primate.

The details of the sensory innervation of the superficial soft tissues of the face are fully known for man. Structures in the forehead and superficial to the anterior part of the lower jaw are supplied respectively by branches of the ophthalmic and mandibular divisions of the trigeminal nerve, while those of the cheek and upper lip receive sensory fibres from the maxillary division. A few of the latter travel in the zygomatico-facial nerve, which supplies a small area of skin on the prominence of the cheek; the remainder are conveyed by the infraorbital nerve which, on emerging from the infraorbital foramen, divides into groups of palpebral, nasal and labial branches. The first group supplies the medial part of the lower eyelid; the second is distributed to the skin of the side of the nose together with the movable part of the nasal septum, while the third ramifies under the skin of the anterior part of the cheek and upper lip. Some of the labial branches are fasciculated with twigs of the facial nerve, and although their function does not appear to have been established experimentally, it would seem possible that they convey proprioceptive impulses from the facial muscles.

Few details are at present available about the maxillary nerve in lower primates. Its topography appears to have received scant attention in classical studies, and even the most modern monographs contain but sketchy accounts of its distribution. For instance, Raven (1950), in the most extensive recent account of the anatomy of the gorilla, figures two specimens of this ape in which branches of the infraorbital nerve pass to the side of the nose and to the upper lip, but does not mention whether any branches supply the lower eyelid or become fasciculated with twigs of the seventh nerve. Again, in their work on the rhesus monkey (*Macaca mulatta*), Hartman & Straus (1933) merely note that after an initial subdivision of the maxillary nerve on the orbital floor, groups of branches similar to those in man emerge from the infra-orbital

foramen, some forming a plexus with twigs of the facial nerve. The maxillary nerve in prosimians appears to have received even less attention than in other sub-human primates. Occasional text figures (e.g. as given by Le Gros Clark (1926) for the tree shrew (*Ptilocercus lowii*)), do however show that branches are distributed to the rhinarium and to that region of the upper lip bearing the mysticial vibrissae.

The purpose of the present study has been to examine the distribution of the maxillary nerve in representatives of as many primate species as could be obtained, and to enquire whether the distribution is affected by variations in the development of a rhinarium, vibrissae, facial muscles and other related structures.

MATERIALS AND METHODS

Anatomical material

The species studied, named according to the scheme outlined by Simpson (1945), together with the numbers of specimens dissected are listed in Table 1. Although in many cases the available material was less extensive than could be desired, the only major groups not represented are the Tarsiiformes, comprising the one extant genus *Tarsius*, and the Daubentonoidea, containing only the Aye-aye.

TABLE 1. The numbers and genera of primates studied

	Genera studied	Vernacular names	Number of specimens
Prosimii	*Tupaia*	Tree shrew	1
	Lemur	Common lemur	1
	Nycticebus	Slow loris	1
	Galago	Bush baby	3
Ceboidea	*Aotes*	Douroucouli	1
	Callicebus	Red titi monkey	2
	Pithecia	Saki monkey	1
	Lagothrix	Woolly monkey	2
	Saimiri	Squirrel monkey	1
	Callithrix	Marmoset	7
	Leontocebus	Tamarin	3
Cercopithecoidea	*Macaca*	Rhesus monkey	4
	Comopithecus	Sacred baboon	2
	Cercopithecus	Guenon	3
Hominoidea	*Pan*	Chimpanzee	1
	Pongo	Orang-utan	1
	Homo	Man	3

Dissection

Either the right or left maxillary nerve was dissected throughout its course from the trigeminal ganglion to the face. Note was made of (1) the point at which the zygomatic nerve took origin (2) the relative sizes of the zygomatic

and infraorbital nerves, (3) the origins of the superior dental nerves, (4) the point at which the infraorbital nerve split into its main divisions, (5) the distribution of the infraorbital nerve, (6) the degree of fasciculation between its branches and those of the seventh (facial) nerve.

Anatomical nomenclature

In all the forms dissected, the zygomatic and superior dental nerves and the branches connecting the maxillary nerve to the spheno-palatine ganglion appeared homologous with the corresponding nerves as described in standard text-books of human anatomy. On the other hand, the customary division of the human infraorbital nerve into nasal, palpebral and labial branches, does not accord fully with the nomenclature used by other comparative anatomists (e.g. Sisson, 1930). Since the palpebral twigs, when present, are closely associated with the nasal branch, the obvious course in the present study was to refer in the first place to nasal and labial divisions of the infra-orbital nerve.

RESULTS

TREE SHREW, LEMUR, LORIS AND GALAGO (PROSIMII) (Fig. 1).

Zygomatic nerve

General description: After leaving the cranial cavity, the maxillary nerve enters the orbit and immediately gives off a zygomatic branch which is much smaller than the main nerve trunk. This zygomatic nerve passes laterally, pierces the base of the post-orbital bar, and emerges on to the cheek where it supplies a small area of skin and the small group of genal vibrissae.

Variation: In the single available specimen of *Nycticebus* the zygomatic nerve divided before reaching the post-orbital bar, one branch piercing the bone and two others passing posterior to it. In two of the three specimens of *Galago* the entire nerve passed posterior to the post-orbital bar.

Dental nerves

General description: As the infraorbital nerve passes forward on the floor of the orbit, it gives off laterally a small superior dental nerve. This divides into anterior and posterior branches which are distributed to the teeth of the upper jaw. The anterior branch runs forward for some distance on the lateral side of the infraorbital nerve.

Variation: In one of the three specimens of *Galago* two superior dental nerves arose together from the maxillary trunk, and in all three representatives of this genus the superior dental nerves appeared to split into a greater number of terminal branches than in the other three prosimian genera.

Passage through infraorbital canal

General description: In prosimians the infraorbital canal is very short and opens on to the face by a single foramen. The infraorbital nerve enters the internal opening of the canal as a single trunk.

Variation: In *Tupaia*, *Lemur* and *Nycticebus* the infraorbital nerve split

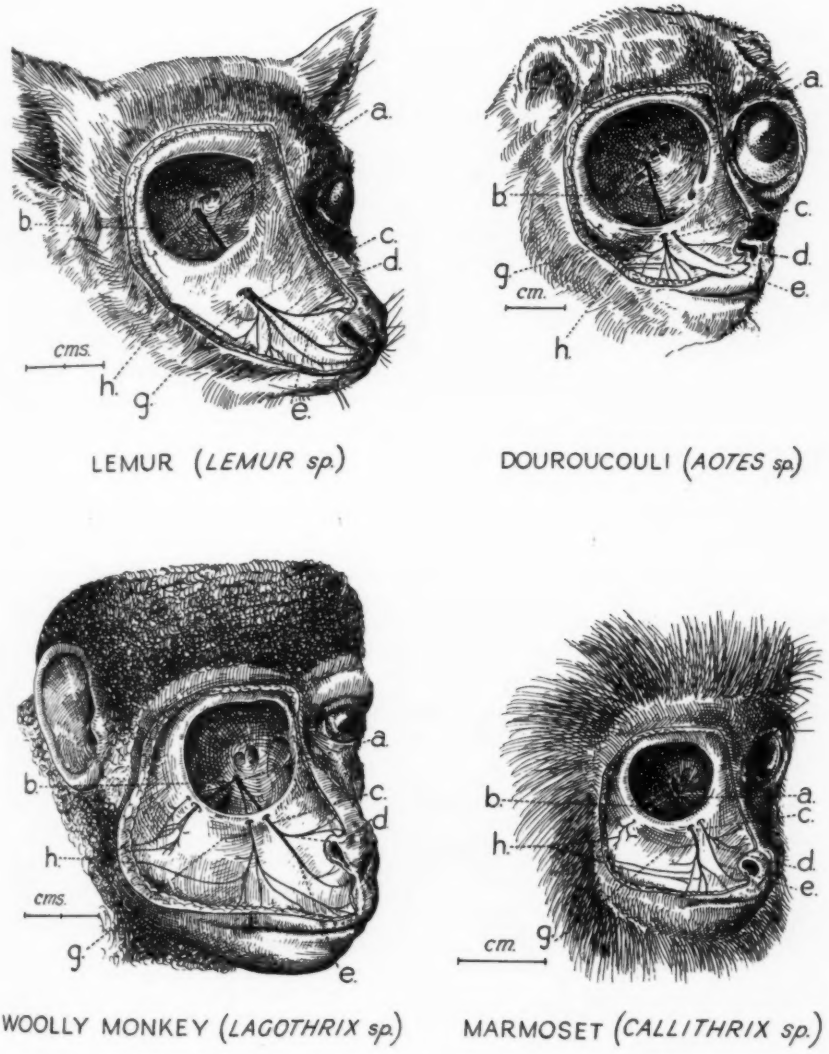

Fig. 1.—The maxillary nerve in prosimians and New World monkeys. (*a*) Infraorbital nerve. (*b*) Zygomatic nerve. (*c*) Nasal division of infraorbital nerve. (*d*) Superior branch of nasal division of infraorbital nerve. (*e*) Inferior branch of nasal division of infraorbital nerve. (*f*) Palpebral twigs. (*g*) Labial division of infraorbital nerve. (*h*) Twigs of the facial nerve which become fasciculated with those of the labial division of the infraorbital nerve. (Muscular branches of the seventh nerve have been removed).

into nasal and labial divisions while in the infraorbital canal. In each of the three specimens of *Galago*, the division occurred after the nerve had emerged on to the face.

Facial distribution

General description: The nasal division splits into a superior nasal branch and a bigger inferior nasal branch. The first ramifies on the dorsum of the nose and supplies the medial part of the rhinarium. The second supplies the lateral part of the rhinarium together with the vestibule of the nose. The central and downwardly extending part of the rhinarium appears to be supplied by a twig of the nasal division which arises before the separation into superior and inferior branches, and whose fibres run for much of their course with the most medial branch of the labial division.

The labial division splits into two groups of branches. The one is distributed to the skin of the cheek while the other supplies the upper lip and the mysticial vibrissae, one twig reaching the lateral part of the philtrum.

One or two fine filaments of the branch of the labial division supplying the cheek become fasciculated with twigs of the seventh (facial) nerve, thus forming a relatively simple infraorbital plexus.

Variation: The three available specimens of the genus *Galago* belonged to the species *senegalensis*. In this type, as pointed out by Boyd (1932), although the downwardly projecting part of the rhinarium is much narrower than in other prosimians, it is not completely submerged by the ingrowth of the maxillary processes, a deep medial groove persisting even in the adult. Nevertheless the branch of the nasal division which in other Prosimii supplies the median downgrowth was not found in any of the three dissections.

In the single available specimen of *Tupaia* the mysticial vibrissae were somewhat more numerous than in the other genera examined, but no corresponding differences were observed in the relative sizes of the associated twigs of the labial division.

NEW WORLD MONKEYS (CEBOIDEA) (Fig. 1)

Zygomatic nerve

General description: The zygomatic nerve arises as the maxillary trunk enters the orbit. It passes laterally across the orbital floor and emerges on to the face through the zygomatico-facial foramen.

Variation: In New World monkeys, the relative sizes of the zygomatic and infraorbital nerves vary widely. In the available specimens of *Aotes*, *Callicebus* and *Pithecia* the zygomatic nerve was, in relation to the infraorbital, as small as in the Prosimii. In the two specimens of *Lagothrix*, in the one of *Saimiri* and in the single specimen of *Ateles* dissected by Anthony (1946) the zygomatic nerve was as big as the infraorbital and carried most of the fibres which after emerging on the face, were fasciculated with twigs of the seventh nerve. In *Callicebus* (seven specimens) and *Leontocebus* (three specimens) the zygomatic nerve was of intermediate size.

These differences have been analysed in detail in a separate study (Oxnard, 1957).

Dental nerves

General Description: In contrast to anatomical arrangements in prosimians, the posterior and anterior superior dental nerves of New World monkeys arise separately. The former are exceptionally fine and leave the main trunk as the maxillary nerve enters the orbit, passing into foramina on the posterior surface of the maxilla. The anterior superior dental nerve arises anteriorly on the orbital floor and runs for some distance along the lateral side of the infra-orbital nerve before diverging into a bony canal which passes antero-laterally towards the teeth.

Variation: In all ten specimens of the Callithricidae (*Callicebus* and *Leontocebus*) the anterior superior dental nerve received from one to four branches from the zygomatic nerve. In two of the three available specimens of *Leontocebus* additional rootlets from the main maxillary trunk joined the anterior superior dental nerve. In these genera, the anterior superior dental nerve subdivided before entering its bony canal.

Passage through infraorbital canal

General description: The infraorbital nerve splits into nasal and labial divisions while in the floor of the orbit. Each enters a separate infraorbital canal which opens on the facial surface of the maxilla by a single infraorbital foramen.

Variation: In one of the two dissections of *Lagothrix*, the lateral infraorbital canal split, the labial division of the nerve emerging through two infraorbital foramina. In one of the three specimens of *Leontocebus* both medial and lateral canals split and both the nasal and the labial divisions of the infraorbital nerve emerged through two separate foramina. On the other hand, in one of the seven specimens of *Callithrix* a single canal transmitted both divisions of the infraorbital nerve.

Facial distribution

General description: Relative to the labial division the nasal is, in New World monkeys, smaller than in prosimians and divides into a small superior nasal branch supplying the skin of the dorsum of the nose, and a bigger inferior nasal branch supplying the vestibule.

The labial division separates into a medial group of branches which supply the philtrum, some twigs passing across the midline to interdigitate with those of the opposite side. An intermediate branch supplies the lip and mystical vibrissae, while most twigs arising from the lateral branch join with the facial nerve.

In New World monkeys relatively more fibres of the infraorbital (or zygomatic) nerve are fasciculated with those of the facial than in the Prosimii.

Variation: With the exception of *Lagothrix* and *Saimiri* the nasal division was much smaller than the labial in all the genera dissected. In the two exceptional cases, the zygomatic nerve was big and the labial division consequently smaller than the nasal.

OLD WORLD MONKEYS (CERCOPITHECOIDEA) (Fig. 2)

Zygomatic nerve

General description: The zygomatic nerve leaves the main trunk of the maxillary nerve as this crosses the pterygopalatine fossa, and together with the much bigger infraorbital nerve, passes through the inferior orbital fissure. It then courses laterally across the floor of the orbit and divides into zygomatico-temporal and zygomatico-facial branches. The former supplies an area of skin over the temporal fossa, the latter the area around the outer canthus.

Variation: In two of the four rhesus monkeys (*Macaca mulatta*) there was no zygomatico-temporal nerve; instead a branch of the zygomatico-facial division ran posteriorly to supply an area of skin over the temporal fossa.

Dental nerves

General description: The posterior superior dental nerves are given off laterally as the maxillary trunk crosses the pterygopalatine fossa, and, as in New World monkeys, enter canals on the posterior surface of the maxilla. The anterior superior dental nerve springs from the labial division of the main infraorbital trunk as this enters the infraorbital groove, and both nerves pass forward into the infraorbital canal. Here, the anterior superior dental nerve diverges from the main trunk to supply the incisor and canine teeth.

Variation: No variations were noted in the mode of origin of the superior dental nerves in any of the Old World monkey specimens available for examination.

Passage through infraorbital canal

General description: While in the infraorbital groove the infraorbital nerve splits into nasal and labial divisions. The labial division then gives off a small lateral and a big medial branch. These, together with the nasal division pass forward to the internal apertures of the three infraorbital canals, which are arranged in a characteristic pattern. The medial (nasal) opening is situated superomedially; the central aperture, conveying one branch of the labial division, is the biggest of the three, while the small lateral opening, conveying the remainder of the labial division, lies in the lateral wall of the infraorbital groove.

Variation: In the four rhesus monkeys (*Macaca mulatta*) the nasal division emerged through a single infraorbital foramen. In each of the two available baboons (*Comopithecus*) and in two of three guenons (*Cercopithecus* sp.) the medial branch of the canal split, the nasal division consequently emerging through two separate foramina. In one rhesus monkey (*Macaca mulatta*), the most lateral of the internal openings was absent, the two branches of the labial division passing into a single canal and emerging through a single infraorbital foramen.

In both baboons, and in one rhesus monkey, the more medial of the canals conveying the labial division divided and labial branches emerged through three separate foramina.

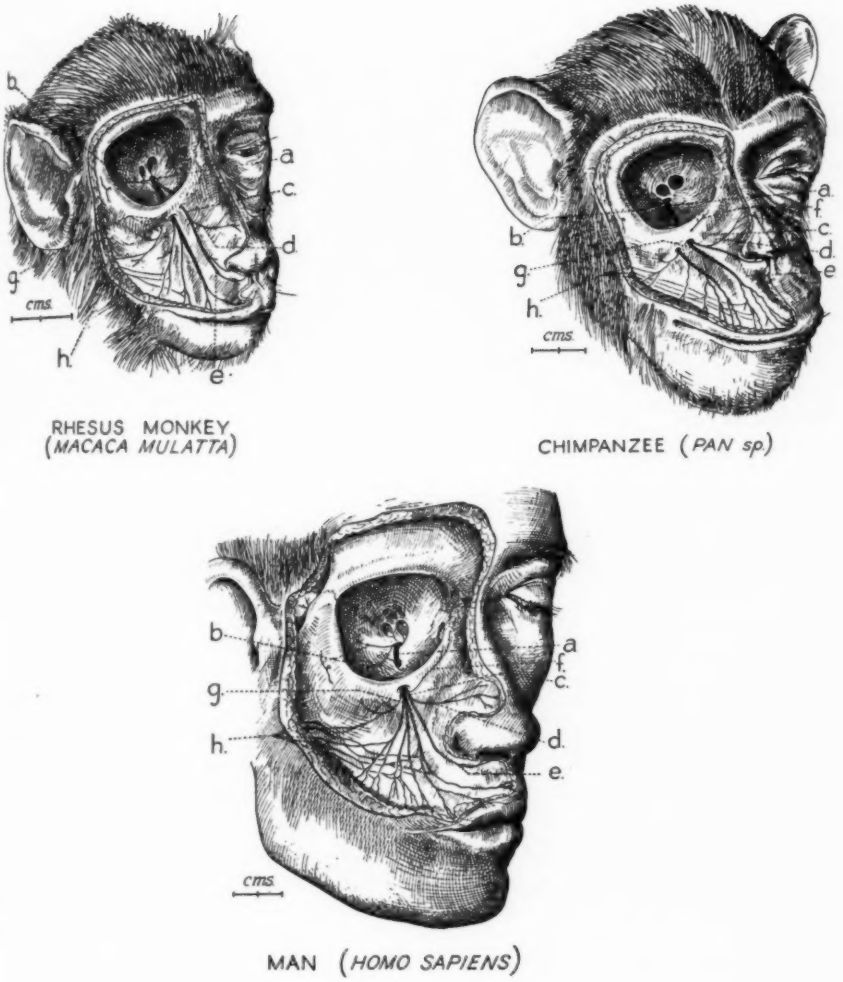

Fig. 2.—The maxillary nerve in Old World monkeys and hominoids. (*a*) Infraorbital nerve. (*b*) Zygomatic nerve. (*c*) Nasal division of infraorbital nerve. (*d*) Superior branch of nasal division of infraorbital nerve. (*e*) Inferior branch of nasal division of infraorbital nerve (*f*) Palpebral twigs. (*g*) Labial division of infraorbital nerve. (*h*) Twigs of the facial nerve which become fasciculated with those of the labial division of the infraorbital nerve. (Muscular branches of the seventh nerve have been removed.)

Facial distribution

General description: The nasal division splits into two. The superior branch supplies the dorsum of the nose and is very fine; the inferior supplies the vestibule and is somewhat bigger.

The labial division splits into medial and lateral branches of which the medial subdivides into three twigs. Of these the most medial supplies the philtrum, some filaments crossing the midline, while the two lateral twigs supply the skin of the upper lip and the anterior part of the cheek. Many fibres of the lateral twigs are fasciculated with filaments of the facial nerve. Other twigs, derived from the subdivisions of the medial branch supplying the lip and cheek, also join with the seventh nerve.

The relative numbers of fibres which become fasciculated with twigs of the facial nerve, while considerably greater than in the Prosimii, are not appreciably different from those found in New World monkeys.

Variation: Apart from such variations as resulted from the splitting of either the nasal or labial division while still in the infraorbital canal, the arrangement of the facial branches of the infraorbital nerve was similar in all the Old World monkey specimens at our disposal.

APES AND MAN (HOMINOIDEA) (Fig. 2)

Zygomatic nerve

General description: The zygomatic nerve is much smaller than the infraorbital nerve, and as in the Cercopithecoidea separates from the maxillary nerve in the pterygopalatine fossa. It crosses the orbital floor and divides into zygomatico-temporal and zygomatico-facial branches which emerge through separate foramina to supply areas of skin over the temporal fossa and near the outer canthus respectively.

Variation: In the single available orang-utan there was no zygomatico-temporal branch, and in one of the three human dissections the zygomatico-temporal and zygomatico-facial nerves arose independently, the former in the pterygopalatine fossa, the latter after the main trunk had entered the orbit.

Dental nerves

General description: The posterior superior dental nerves leave the maxillary trunk as it crosses the pterygopalatine fossa, and enter foramina on the posterior surface of the maxilla. The anterior superior dental nerve originates from the infraorbital nerve on the floor of the orbit.

Variation: None of the five available specimens exhibited any variation in the mode of origin of the anterior superior dental nerve. Although Fitzgerald (1956) regards the presence of a middle superior dental nerve as a common occurrence in man, this was not found in any of the three human, or in either of the ape specimens studied. However, in one of the human dissections a branch of the nasal division of the infraorbital nerve which lay deep on the face passed into a canal which opened on to the facial surface of the maxilla supero-medial to the tip of the root of the canine tooth. This canal passed at first infero-medially and then supero-medially. The canal and its contained

nerve then divided into two, one branch supplying the lacrimal duct and the other being distributed to the roots of the incisor teeth. This bony canal lay anterior to the canalis sinuosus (Wood Jones, 1939) which contained the anterior superior dental nerve.

Passage through infraorbital canal

General description: The infraorbital nerve enters the single internal opening of the infraorbital canal and for much of this part of its course comprises a number of interlacing bundles.

Variation: In each of the three human dissections there was a single infraorbital foramen and the infraorbital nerve separated into nasal and labial divisions as it lay under cover of M. levator labii superioris after emerging from the infraorbital foramen.

In the chimpanzee specimen, the infraorbital canal divided into two main branches. The medial one conveyed the nasal division of the infraorbital nerve together with some fibres of the labial division, while the lateral canal conveyed the remainder of the labial fibres. From the medial canal there arose a small canal which was directed upwards, and conveyed the palpebral twigs.

In the orang-utan specimen, the infraorbital canal first split into medial and lateral branches, the nasal division of the infraorbital nerve being conveyed by the medial, and the labial division by the lateral canal. This latter then split into three, and from the most medial of these sub-divisions, three small canals passed deeply to open on the surface of the face below the four main infraorbital foramina.

Facial distribution

General description: The nasal division is smaller than the labial. It has a small superior branch which supplies the dorsum of the nose, and a bigger inferior branch which passes deep to supply the vestibule. Palpebral twigs pass upwards to supply the skin of the medial part of the lower eyelid. The labial division provides (1) a small medial branch which passes to the philtrum, some twigs crossing the midline to interdigitate with those from the opposite side, (2) a big intermediate group of branches supplying the lip, and (3) a smaller lateral group of branches ramifying under the skin of the cheek. Each branch of the labial division appears to give rise to far more small twigs than is the case in prosimians or monkeys.

Many of the fibres from the branches supplying the cheek are fasciculated with twigs of the facial nerve, and the infraorbital plexus thus formed is more complex than in monkeys or prosimians.

Variation: The one available orang-utan differed from the chimpanzee and the three human specimens in that the branch supplying the philtrum, which normally originates from the labial division, remained fasciculated with the nasal division after the initial subdivision of the main infraorbital trunk.

In the chimpanzee, the palpebral twigs arose from the nasal division of the infraorbital nerve in the infraorbital canal, while in the orang-utan they took origin from this branch after its emergence on to the face. In the three human

dissections the nasal, labial and palpebral branches arose practically simultaneously as the infraorbital nerve emerged on to the face. However, the palpebral twigs were always closely associated with the medial side of the nasal division and in two of the three specimens their point of origin was noticeably distal to the main subdivision of the infraorbital nerve.

In each of the three human specimens, the infraorbital plexus was far more extensive than in either ape examined.

DISCUSSION

The dissections analysed in this study, although too few to permit anything more than tentative generalizations about the branches of the maxillary nerve in different primate groups, or to give a satisfactory picture of minor variations in their distribution, indicate that a basic arrangement exists within the order.

The zygomatic nerve and (in all groups except the Prosimii) the posterior superior dental nerves, originate from the main trunk very shortly after its emergence from the cranial cavity. The anterior superior dental nerve arises as the infraorbital trunk passes forward on the orbital floor, and a final separation into nasal and labial divisions occurs either in the infraorbital canal or after the nerve has emerged on to the face. Branches of the nasal division are distributed in the main to the rhinarium or to the vestibule of the nose, these structures being presumed derivatives of the embryonic frontonasal, process (Boyd, 1932). On the other hand, those of the labial division are chiefly associated with structures derived from the maxillary process (i.e. the skin of the cheek and upper lip together with the mysticial vibrissae) and with the facial muscles.

Certain variations are superimposed upon this pattern. One concerns the point at which the infraorbital nerve splits into nasal and labial divisions, this in turn affecting the number of internal openings of the infraorbital canal. In prosimians, where the nerve divides only after emerging on to the face, the short infraorbital canal has only one internal opening. In monkeys, the nerve divides while crossing the orbital floor, and in New World species there are, as a rule, two internal openings, one transmitting the nasal division and the other the labial. In Old World species, where the labial division splits while still on the orbital floor, there are usually three internal foramina. In the Hominoidea, where the initial division of the nerve takes place either in the canal or after the nerve has emerged on to the face, there is again a single aperture.

These differences, together with variations in such features as the number of external openings of the infraorbital canal, are of taxonomic interest, but have no obvious functional significance. On the other hand, although it has not been possible to establish whether or not variations in the development of the mysticial vibrissae affect the distribution of the infraorbital nerve fibres, it is evident that variations in the relative sizes of the nasal and labial divisions of this nerve are closely correlated with differences in the development of a rhinarium and with variations in the complexity of the facial musculature. Thus when as in the tree shrew, lemur, loris and galago, a well developed rhinarium is associated with relatively undifferentiated facial muscles, the

labial division is smaller than the nasal and relatively few fibres are fasciculated with twigs of the seventh nerve. When, as in monkeys, there is no rhinarium and the facial muscles are relatively complex, the labial division is the bigger and more of its fibres are associated with twigs of the seventh nerve. In apes, where vibrissae have been eliminated and the facial muscles still further elaborated, the infraorbital plexus becomes more extensive than in monkeys, while in man, where the mimetic musculature reaches the peak of its development, fibres of the labial division of the infraorbital nerve make a still greater contribution to the infraorbital plexus.

This general picture does not appear to be influenced by the development of facial structures such as the cheek pouches of Old World monkeys, nor by such reductions in size of the labial nerve as occur in some New World monkeys, because in these forms many of the presumably proprioceptive fibres reach the facial muscles through an enlarged zygomatico-facial nerve (Oxnard, 1957).

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SUMMARY

1. The maxillary nerve has been dissected throughout its course in representatives of the Prosimii (tree shrew, lemur, loris and galago); the Ceboidea (New World monkeys); the Cercopithecoidea (Old World monkeys), and the Hominoidea (chimpanzee, orang-utan and man).

2. The maxillary trunk gives off the zygomatic and superior dental nerves before splitting at a variable point into nasal and labial divisions. The first is distributed to the side and vestibule of the nose and supplies the rhinarium if present. The second is distributed to the mystical vibrissae (if present) and to the skin of the cheek and upper lip—some of its branches being fasciculated with twigs of the facial nerve.

3. In the Prosimii, where a rhinarium is associated with an uncomplicated facial musculature, the nasal division is the bigger. Relatively few fibres of the labial division are fasciculated with twigs of the seventh nerve.

4. In monkeys where the rhinarium has disappeared and the facial musculature has increased in complexity, the labial division is the bigger and more of its fibres are associated with twigs of the facial nerve. In certain New World monkeys (*Lagothrix*, *Saimiri* and *Ateles*) many of these presumably proprioceptive fibres travel via the zygomatico-facial nerve.

5. The further elaboration of the facial musculature in apes results in still more fibres being fasciculated with twigs of the seventh nerve, while in man, the trend continues further and the infraorbital plexus is more extensive than in any lower primate.

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THE INFRAORBITAL FORAMEN IN THE HOMINOIDEA

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(With 5 plates)

CONTENTS

	Page
Introduction	471
Materials and methods	473
Skulls	473
Age sub-groups	473
Sex sub-groups	473
Morphological observations	474
Biometry	474
Measurement	474
Precision of measurement	474
Statistical analysis	474
Basic data	474
Grouping of data	474
Precision of estimates	475
Comparison	475
Results	475
Numbers of foramina	475
Adult men	475
Adult apes	475
Age changes in numbers of foramina	477
Arrangement of foramina	477
Position of foramina in adults	478
Main apertures	478
Centre of group of foramina	478
Age changes in position of foramina	478
Discussion	480
Acknowledgments	483
Summary	483
References	484
Explanation of plates	484

INTRODUCTION

The distribution of the maxillary nerve is basically the same throughout the primates (Ashton & Oxnard, 1958). The main trunk first gives off a zygomatic branch which supplies an area adjacent to the outer canthus of the eye. The remaining fibres form the infraorbital nerve, which passes forwards on the floor of the orbit, giving branches to the teeth of the upper jaw, and splitting at a variable point into nasal and labial divisions. These emerge through the infraorbital foramen, the nasal division giving branches to the vestibule of the nose and to the rhinarium, when present, and the labial division

supplying the skin of the anterior part of the cheek, the mystical vibrissae and upper lip. Some fibres become fasciculated with twigs of the seventh nerve. In species with a well-developed rhinarium, the nasal division is bigger than the labial. Conversely, if the facial muscles are highly differentiated it is the labial division which is the more prominent.

In monkeys, apes and man the zygomatic nerve is given off as the maxillary nerve crosses the pterygopalatine fossa. After entering the orbit by way of the inferior orbital fissure, the nerve courses laterally across the orbital floor, penetrating the zygomatic bone, finally emerging through the zygomatico-facial foramina. The infraorbital nerve also passes through the inferior orbital fissure, and lies, together with its associated blood vessels, in a forwardly-directed groove in the floor of the orbit. The anterior part of this groove is roofed over to form the infraorbital canal which opens on the facial surface of the maxilla at the infraorbital foramen, and transmits the big labial and smaller nasal division of the infraorbital nerve.

Two main variations of this basic plan are found in the Anthropoidea (Ashton & Oxnard, 1958). The first concerns the sizes of the zygomatic and infraorbital nerves. In most species, the zygomatic nerve is relatively small, but in the spider monkey (*Ateles* sp.) the squirrel monkey (*Saimari* sp.), and the woolly monkey (*Lagothrix* sp.) (Anthony, 1946; Oxnard, 1957) it is bigger than the infraorbital nerve, and not only supplies its usual area of skin but also gives off fibres which become fasciculated with twigs of the facial nerve. In other species the corresponding fibres travel *via* the infraorbital nerve.

The second variation concerns the route by which branches of the infraorbital nerve reach the various areas of the face. In monkeys, the nerve splits while lying in the infraorbital groove, and there are either two or three infraorbital canals, each arising from the anterior end of the infraorbital groove a short distance posterior to the inferior orbital margin. With the further subdivision of their contained nerves, some of these infraorbital canals divide and open on the facial surface of the maxilla by several infraorbital foramina. In many monkeys these openings are linearly disposed below the inferior orbital margin. In baboons, they are disposed irregularly over the surface of the snout.

In Anthropoid apes, the infraorbital nerve normally splits into nasal and labial divisions while in the infraorbital groove, and both pass through the single internal aperture of the infraorbital canal. In the gibbon this opening lies immediately below and posterior to the sharply upturned lower border of the orbit, but in the great apes the aperture is some distance posterior to the inferior orbital margin. The number of external openings varies. In the gibbon the foramen may be single or double, and lies relatively close to the inferior orbital margin. In the gorilla, although a single foramen is not uncommon, two infraorbital apertures are usually present, both lying much further from the orbital margin than in the gibbon. At least two external foramina occur in the chimpanzee, whilst in the orang-utan there may be as many as six, all lying relatively far down the facial skeleton.

In man, the trunk of the infraorbital nerve passes through a single infraorbital canal whose internal opening lies some distance posterior to the inferior orbital margin. The nerve usually divides only after having emerged on the face through a single foramen lying close below the inferior orbital margin. Occasionally the canal subdivides, and there is then a second and much smaller external opening.

The frequencies with which different numbers of external infraorbital foramina occur have been described in several recent papers (Man: Riesenfeld, 1956; Apes: Schaefer, 1954; Schultz, 1954). These studies do not, however, attempt to explain why the observed differences occur. Because of this, it is uncertain what weight needs to be attached to the observation that a single infraorbital foramen is usual in the South African fossil Australopithecinae (Broom & Schepers 1946; Le Gros Clark, 1949; Schultz, 1954). In an effort to illumine this question, the present study discusses the possible correlation between the numbers of foramina, their position on the maxilla and the general proportions of the facial skeleton.

MATERIALS AND METHODS

Skulls

One hundred and ninety-two human, 205 gorilla, 178 chimpanzee and 82 orang-utan skulls of varying age were available for study. Sixty-four adult gibbon skulls, assigned to a total of thirteen species, were also examined.

The gorilla and chimpanzee skulls belonged to the collections of the Powell-Cotton Museum, Birchington. The orang-utans were from the Department of Zoology, British Museum (Natural History), and the Department of Anatomy University of Birmingham. The adult human skulls comprised approximately equal numbers of West African natives, Australian aboriginals and modern whites taken at random from the collections of the Department of Physical Anthropology, British Museum (Natural History), and the Cambridge University Museum of Archaeology and Ethnology. Such immature human skulls as were studied were of unknown stock, and belong to the Department of Anatomy, University of Birmingham.

Age sub-groups

Human and great ape skulls were divided into four dental age sub-groups:

(a) (Men and apes): stages up to and including the completion of the milk dentition.

(b) (Men): milk teeth with the first permanent molars and/or incisors erupting or erupted.
(Apes): milk teeth with the first permanent molars erupting or erupted.

(c) (Men and apes): stages between (b) and (d).

(d) (Men and apes): adults with all the permanent teeth erupted.

Sex sub-groups

The sexes of the chimpanzee and gorilla skulls were known from field records, and those of the adult orang-utans were inferred from an examination of the

customary anatomical features. No attempt was made to sex any human, gibbon or immature orang-utan skulls.

Morphological observations

The numbers of infraorbital foramina in both left- and right-hand maxillae were counted, each aperture having first been probed with a bristle in order to check that it did, in fact, communicate with the infraorbital canal and was not merely a nutrient foramen. For each age and sex sub-group, the percentages of individuals having one, two, three or more foramina were then computed.

Note was made of the direction in which each aperture pointed, and in maxillae with more than one foramen, the relative sizes and positions of the various openings were recorded.

Biometry

Measurement

Measurements were made with calipers: (1) in a direction parallel to the sagittal plane, from the centre of the sharp upper border of each infraorbital foramen to the orbital margin; (2) in a direction parallel to the sagittal plane from the centre of the sharp upper border of the biggest infraorbital foramen to the alveolar margin; (3) in a direction perpendicular to the alveolar margin, from the centre of the sharp upper border of each infraorbital foramen to the alveolar margin.

Two indices were computed to indicate the position of the biggest infraorbital foramen in every skull studied. The first expressed the distance of the foramen from the orbital margin as a percentage of its perpendicular distance from the alveolar margin. The second expressed the distance from the orbital margin as a percentage of that from the alveolar margin, as measured parallel to the sagittal plane. A third index indicated the position of the centre of the group of infraorbital foramina, and was calculated by expressing the average distance from the orbital margin as a percentage of the average perpendicular distance from the alveolar margin.

Precision of measurement

Measurements were recorded to the nearest 0·1 cm. Repeat measurements of five adult female gorilla skulls showed that in the case of each index, the differences between skulls were very significantly greater ($P<0{\cdot}001$) than variations due to inconsistencies in measurement, which, it can therefore be assumed, are unlikely to affect the results of the analyses.

Statistical analysis

Basic data: Means and standard errors were computed (a) for the numbers of foramina and (b) for each of the three indices in each age and sex sub-group.

Grouping of data: Data from the right and left sides were first examined separately. Preliminary comparisons showed that for each age and sex subgroup of each type of ape and man, the average number of foramina was the same in the left- and right-hand maxillae, and that on an average, the position

of the openings relative to the orbital and alveolar margins was similar on the two sides. Subsequent analyses were, therefore, based on data derived from the maxilla of the right side.

Analysis also showed that both as regards the average number of foramina and their position on the face, there were no differences either among the series of adult British, West African and Australian aboriginal skulls, or between male and female ape skulls of corresponding age. For the purposes of further comparison, all adult human skulls, and in the case of each species of ape, male and female skulls of comparable age were therefore pooled.

Precision of estimates: Judging by the ratios of the standard errors of the means to the means themselves, the estimates derived from the available samples were not as precise as those which usually characterize studies of this type. Thus in the seventeen estimates of the numbers of foramina (one in each of the four age sub-groups of chimpanzee, gorilla, orang-utan and man, and one for adult gibbons), the standard error of the mean was less than five per cent of the mean itself in only seven instances, and lay between five and ten per cent in another seven.

In the case of the fifty-one estimates derived from the three indices (three in each of the four age-groups of chimpanzee, gorilla, orang-utan and man, and three for adult gibbons), the standard error of the mean was less than five per cent of the mean itself in twenty-nine cases, and lay between five and ten per cent in twenty instances. In spite of this relative imprecision, analysis revealed that the estimates were, in most cases, adequate to show that differences between age groups and between species were significant statistically.

Comparison: Comparisons were made by means of t tests and analyses of variance between the numbers of foramina in apes and man of corresponding age and between different age groups of each genus. Corresponding comparisons were also made for each index.

RESULTS

Numbers of foramina

Adult men

On an average there were 1·05 infraorbital foramina in each of the 153 adult human maxillae examined in this study. This figure is less than the value of 1·08 given by Schultz (1954), or the mean of the range of 1·04—1·22 given by Riesenfeld (1956) for twenty-seven " races " of modern men. The difference may, on the one hand, be due to the particular racial composition of our sample. Alternatively, it might be attributable to an error in random sampling, the 153 skulls examined in the present study being far fewer than the 1,038 listed by Schultz, or the 8,836 examined by Riesenfeld.

In the present study, two ipsilateral infraorbital foramina were found in five skulls, and four such foramina in one.

Adult apes

For each species of ape, both the percentages of individuals with one, two, three or more foramina and also the average numbers of apertures were similar

TABLE 1

The numbers of infraorbital foramina in adult apes. Combined data from the present study and from Schultz (1954).

Species (Male+Female)	No. of skulls	Average number of foramina	PERCENTAGE WITH						
			1 Foramen	2 Foramina	3 Foramina	4 Foramina	5 Foramina	6 Foramina	7 Foramina
Gibbon	243	1·23	79·0	19·3	1·6	0·0	0·0	0·0	0·0
Gorilla	227	1·59	46·3	48·5	4·8	0·4	0·0	0·0	0·0
Chimpanzee	317	2·41	10·1	49·2	30·9	9·5	0·3	0·0	0·0
Orang-utan	137	3·32	3·6	20·4	38·7	21·2	10·9	3·6	1·5

to the figures recorded by Schultz (1954). In order, therefore, to give as comprehensive a picture as possible, Schultz's figures have been combined with our own, the overall results being presented in Table 1.

The gibbon has, on an average, 1·2 foramina in each maxilla, the gorilla 1·6; the chimpanzee 2·4; and the orang-utan 3·3.

Almost eighty per cent of gibbons have a single foramen, double apertures being found in most of the remainder. On the other hand, some fifty per cent of gorillas have two apertures in one or both maxillae, rather fewer having a single foramen on one or both sides. Two ipsilateral foramina are also found in approximately fifty per cent of chimpanzees, but only ten per cent of these apes have a single foramen. The remainder have three or more. Almost forty per cent of orang-utans have three foramina. Twenty per cent have two and another twenty per cent have four. Fewer than five per cent have a single aperture.

Age changes in numbers of foramina

The present study provides no evidence that the average numbers of foramina change during post-natal growth. The figures which suggest that slight increases occur with age in the chimpanzee and gorilla and a slight decrease in the orang-utan are insignificant statistically ($P > 0{\cdot}02$).

Arrangement of foramina

In man, the single infraorbital foramen lies relatively close to the orbital margin and varies in shape from an ellipse (Pl. 1, fig. 1), with its long axis set either horizontally or obliquely, to a circle (Pl. 1, fig. 2). The upper border of the foramen is sharp. The lower border is rounded and fades into the maxillary surface, shallow grooves directed downwards, and in some cases medially, indicating the course of the emergent nerves and blood vessels. If the foramen is duplicated, the second aperture is much the smaller, and usually lies above and medial to the main foramen (Pl. 1, fig. 3).

In the gibbon, the infraorbital foramen is usually elliptical, with its long axis set obliquely, and lies immediately below the orbital margin (Pl. 1, fig. 4). The foramen is normally directed downwards and medially, its upper edge being sharp and its lower border rounded. Where the foramen is duplicated, the smaller foramen usually lies below and lateral to the main aperture (Pl. 1, fig. 5), but occasionally it lies above and medial thereto (Pl. 1, fig. 6).

The main foramen of the gorilla is usually circular, with a sharp upper border, and with shallow grooves radiating from its smooth inferior and medial rims (Pl. 2, figs. 7 & 8). Occasionally the foramen may be partly divided (Pl. 2, fig. 9). In about fifty per cent of specimens, two distinct foramina are present, the smaller aperture usually (Pl. 2, fig. 10), though not invariably (Pl. 2, fig. 11), lying below and lateral to the main foramen. A third and much smaller foramen is occasionally found close to the more lateral of the two principal apertures and its opening may be more laterally directed (Pl. 2, fig. 12).

The characteristics of the main foramen in the chimpanzee are similar to those of the gorilla, and apart from the ten per cent of cases in which the

aperture is single (Pl. 3, fig. 13), there is usually a smaller foramen lying between the main infraorbital opening and the inferior orbital margin. This second foramen is directed upwards and laterally (Pl. 3, figs. 14 & 15). If a third foramen is present, it usually lies lateral to and sometimes below the main aperture (Pl. 3, figs. 16 & 17). Where there are four or more foramina, the additional ones vary in size and lie either lateral or medial to the main openings. In the latter case an orifice may occasionally be directed medially (Pl. 3, fig. 18).

The main foramen of the orang-utan is also like that of the gorilla (Pl. 4, figs. 19 & 20), but except in four per cent of cases there is always at least one additional opening. When only one such additional opening is present, it usually lies infero-lateral to the central one, and is not infrequently the bigger (Pl. 4, fig. 21). In the forty per cent of cases where there are three foramina, the smallest is usually the most lateral, its orifice not infrequently being directed laterally (Pl. 4, fig. 22). The smallest of a group of four or more foramina often lies below the main apertures (Pl. 4, figs. 23 & 24), which themselves may lie along a line parallel to the lower orbital margin (Pl. 4, fig. 24).

Position of foramina in adults

Main apertures

Table 2 records the mean values and standard errors of the indices which describe the positions of the biggest infraorbital apertures, and the centre of the group of foramina, where more than one opening is present.

In adult men (Pl. 5, fig. 25) and gibbons (Pl. 5, fig. 26), the distance between the infraorbital foramen and the inferior orbital margin (i.e. the orbito-foraminal distance), is only about twenty per cent of the distance between the foramen and the alveolar margin (i.e. the orbito-alveolar distance). In the gorilla and chimpanzee, the corresponding figures for the biggest foramen are about forty-five and forty per cent respectively (Pl. 5, figs. 27 & 28). In the orang-utan, the position of the biggest foramen is intermediate between that in man and the gibbon on the one hand, and the gorilla and chimpanzee on the other, the orbito-foraminal distance being some thirty-five per cent of the foramino-alveolar distance (Pl. 5, fig. 29).

Centre of group of foramina

The picture is slightly different if the centre of the group of foramina is taken as the point of reference. As few human maxillae have more than one infraorbital opening, the centre of the group on an average lies close to the biggest foramen. In the chimpanzee, because a small aperture often lies close to the orbital margin, the centre of the group tends to lie above the main foramen in a position somewhat below that characteristic of man and the gibbon. In the orang-utan and gorilla, the centre of the group lies below the main aperture as the smaller foramina in these apes lie lateral to and below the main opening.

Age changes in position of foramen (Table 3)

In skulls in which the milk teeth are erupting, the infraorbital foramen is relatively closer to the inferior orbital margin than in adults. In the gorilla,

TABLE 2

Position of the infraorbital foramen in relation to the orbital and alveolar margins.

TABLE 2

Position of the infraorbital foramen in relation to the orbital and alveolar margins.

Species (Male and female combined)	Age group	Index 1			Index 2			Index 3		
		Mean	No. of observations	S.E. of mean	Mean	No. of observations	S.E. of mean	Mean	No. of observations	S.E. of mean
Man	a	18·6	12	1·38	18·3	12	1·29	18·6	12	1·38
	b	24·9	16	1·08	24·3	16	1·09	24·9	16	1·08
	c	23·6	11	1·50	22·8	11	1·39	23·6	11	1·50
	d	22·7	153	0·53	21·3	153	0·49	22·7	153	0·53
Gibbon	d	20·6	64	0·52	18·4	64	0·49	21·3	64	0·69
Gorilla	a	37·4	18	2·62	31·9	18	2·23	38·6	18	2·85
	b	44·1	21	1·58	38·6	21	1·14	45·3	21	1·46
	c	44·8	30	1·41	38·6	30	1·19	47·7	30	1·19
	d	45·1	136	0·64	39·1	136	0·70	47·7	136	0·62
Chimpanzee	a	29·4	14	2·42	24·4	14	2·11	25·6	14	2·05
	b	36·8	26	1·63	30·2	26	1·37	29·5	26	1·52
	c	33·8	30	1·54	28·4	30	1·38	26·4	30	1·11
	d	37·4	108	0·91	30·3	108	0·75	29·4	108	0·69
Orang-utan	a	15·7	7	1·15	14·6	7	1·11	34·1	7	3·63
	b	19·7	7	1·19	18·3	7	0·99	35·1	7	2·17
	c	22·3	6	2·23	19·0	6	1·61	35·3	6	4·88
	d	32·7	62	0·97	27·7	62	0·80	45·6	62	1·47

For explanation of age sub-groups, see text.

$$\text{Index 1} = \frac{100 \times \text{distance of biggest aperture from orbital margin}}{\text{Perpendicular distance from alveolar margin}}$$

$$\text{Index 2} = \frac{100 \times \text{distance of biggest aperture from orbital margin}}{\text{Distance from alveolar margin measured parallel to sagittal plane}}$$

$$\text{Index 3} = \frac{100 \times \text{Distance of centre of group of foramina from orbital margin}}{\text{Perpendicular distance of centre of group from alveolar margin}}$$

chimpanzee and man, the biggest (or the only) aperture lies some twenty per cent closer to the orbital margin than in older individuals. In these species, the adult foraminal position is attained by the time the first permanent molars are in place. In the orang-utan, on the other hand, the foramen is some fifty per cent closer to the orbital margin when the milk teeth are erupting than it is in adults. In this ape, the relative position of the opening seems to continue changing until maturity is reached.

TABLE 3

Age changes in the position of the infraorbital foramen.

Species Male and female combined	Age-group	Index 1	Index 2	Index 3
Man	a	82	86	82
	b	110	114	110
	c	104	107	104
	d	100	100	100
Gorilla	a	83	82	81
	b	98	99	95
	c	99	99	100
	d	100	100	100
Chimpanzee	a	79	81	87
	b	98	100	100
	c	90	94	90
	d	100	100	100
Orang-utan	a	48	53	75
	b	60	66	77
	c	68	69	77
	d	100	100	100

$$\text{Index 1} = \frac{100 \times \text{Distance of biggest aperture from orbital margin}}{\text{Perpendicular distance from alveolar margin}}$$

$$\text{Index 2} = \frac{100 \times \text{Distance of biggest aperture from orbital margin}}{\text{Distance from alveolar margin measured parallel to sagittal plane}}$$

$$\text{Index 3} = \frac{100 \times \text{Distance of centre of group of foramina from orbital margin}}{\text{Perpendicular distance of centre of group from alveolar margin}}$$

Adult value of each index = 100 units.

For explanation of age sub-groups see text.

DISCUSSION

The present study not only confirms the wide numerical variation in the infraorbital foramina of men and apes, but also shows that there are equally big differences in their arrangement. This variation appears to be unassociated with any corresponding differences in the subdivision of the infraorbital nerve, which always splits into a larger labial and a smaller nasal division. Both divisions subdivide, and whereas in man, the gibbon, and in some fifty per cent of

gorillas, a single foramen transmits their main branches, at other times, as in many chimpanzees and presumably in fifty per cent of gorillas, one foramen transmits the nasal division, together with the medial branches of the labial division, while a second transmits its lateral branches (Ashton & Oxnard, 1958). Alternatively, as sometimes occurs in the orang-utan, several separate foramina convey the lateral branches of the labial division. Again, whilst in the chimpanzee a separate foramen transmits the twigs of the nasal division supplying the lower eyelid, in other apes such twigs emerge through the more medial of the main foramina.

Variations in the numbers of infraorbital foramina also appear to be unrelated to such features as the degree of prognathism. Thus, although a single foramen occurs most frequently in man and the gibbon (the most orthognathous members of the Hominoidea), an undivided opening is also found in almost fifty per cent of gorillas, which are the most prognathous of the great apes. The aperture is also normally single in the fossil Australopithecinae (Table 4) which, in spite of their shorter and more rounded palate, were almost as prognathous as the living great apes.

The number of foramina seems equally unrelated to the length of the infraorbital canal, this being relatively greatest in man, intermediate in the great apes, and least in the gibbon.

Again, the numbers of foramina would appear to have no strong correlation with their position on the maxilla. In the human and the gibbon skull the single infraorbital foramen is relatively close to the inferior orbital margin. In the fossil Australopithecinae, and in gorillas (one in every two having a single foramen) it is relatively far down the face.

Variations in the soft tissues of the face would likewise seem scarcely able to account for the variations in the numbers of foramina. For example, the fibrous cheek pad, so striking a facial feature of the adult male orang-utan, is not related to any peculiarities in the infraorbital foramina, these being arranged exactly as in the female, which has no comparable pad.

Although the possibility cannot be excluded that the numbers of infraorbital foramina may be influenced by other cranial or facial features, the apparent lack of correlation with the more obvious of these would indicate that the numbers and arrangements of the openings may have little functional significance. On the other hand, there is some indirect evidence that the number of foramina is determined genetically. Schultz (1954) figures the skulls of a father, mother and their three children, all of whom had duplicated foramina in one or both maxillae. He also mentions that notable variations occur in the average numbers of foramina in geographically isolated populations of both howler monkeys and gibbons. In addition, Riesenfeld (1956) points to variations in the frequencies with which multiple foramina are found in different human races, and draws attention to an apparent correlation with the number of ethmoidal foramina.

In contrast to the lack of correlation between the numbers of foramina and other facial features, there appears to be a strong relationship between their position on the maxilla and the degree of prognathism. Thus, in the orthognathous gibbon, as in man, the foramen lies close to the inferior orbital

margin. In the prognathous great apes it lies relatively far down the facial skeleton. The location of the foramen may, therefore, have greater taxonomic significance than the number of openings.

It is, therefore, noteworthy that in the available accounts of the anatomy of the fossil Australopithecinae, descriptions of the infraorbital foramen have almost invariably focused on the fact that as in man, and in contrast to the living great apes, there is normally a single foramen in each maxilla. Thus Broom (Broom & Schepers, 1946) writes that " in the orang, and usually in the chimpanzee and gorilla, there is more than one infraorbital foramen. In Australopithecus there is only a single foramen as in man." Le Gros Clark (1949) also lists the single infraorbital foramen of the Australopithecinae as a feature " not commonly found in all the large anthropoid apes, but which may occur sporadically." On the other hand, in their account of *Paranthropus crassidens*, Broom & Robinson (1952) merely mention that the single infraorbital foramen " is situated low down in the facial plate".

TABLE 4

The infraorbital foramen in the australopithecinae

Fossil species	Source of data	No. of infraorbital foramina	
		Right maxilla	Left maxilla
Australopithecus africanus	Broom & Schepers (1946)	1	1
Australopithecus prometheus	Dart (1949)	1	—
Plesianthropus transvaalensis			
S1	Broom & Schepers (1946)	1	—
S2		1	—
S5	Broom, Robinson & Schepers	1	1
S7	(1950)	1	—
Paranthropus robustus	Broom & Schepers (1946)	—	1
Paranthropus crassidens			
SK46	Broom & Robinson (1952)	—	1
SK48		1	1

The data refer to those maxillae for which descriptions or clear photographs are available.
A dash shows that the maxilla was either missing or broken.

In the consistent possession of a single infraorbital foramen, the nine australopithecine specimens which provide information on this point clearly resemble man and the gibbon rather than the great apes (cf. Tables 1 & 4). On the other hand, it needs to be remembered that a single foramen occurs in approximately one in two gorillas. Furthermore, it is significant that, in the fossils, the aperture lay in a position similar to that seen in the gorilla, and much further

down the facial skeleton than in modern man and gibbon, or in the extinct species *Homo neanderthalensis* (cf. Tables 2 & 5). In this hominid, although the face was somewhat more prognathous and the position of the infraorbital foramen correspondingly lower than in modern man, the aperture lay much closer to the orbital margin than is usual in the extant great apes.

TABLE 5

The position of the infraorbital foramen in the Australopithecinae and in Neanderthal Man.

		Age	Index 1	Index 2
Australopithecinae	*Australopithecus africanus*	Milk dentition and first permanent molars	41	42
	Plesianthropus transvaalensis V.	Adult	30	28
	Paranthropus crassidens			
	S.K. 46	Adult	61	60
	S.K. 48	Adult	58	55
	Paranthropus robustus	Adult	59	53
	Average of adults :		52	49
Neanderthal Man	La Chapelle aux Saints	Adult	33	30
	La Férrassie	Adult	25	25
	Gibraltar	Adult	29	28
	Rhodesia	Adult	33	30
	Average		30	28

$$\text{Index 1} = \frac{100 \times \text{Distance of biggest aperture from orbital margin}}{\text{Perpendicular distance from alveolar margin}}$$

$$\text{Index 2} = \frac{100 \times \text{Distance of biggest aperture from orbital margin}}{\text{Distance from alveolar margin measured parallel to sagittal plane}}$$

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We are indebted to the Heads of the Museum and University Departments listed on p. 473 for allowing us to study the material in their charge. Our best thanks are also due to Mr W. J. Pardoe, who prepared the plates, and to Mr S. J. Tranter for technical help when collecting the data. Expenses incurred in the field work were met by a grant from the Wenner-Gren Foundation.

SUMMARY

1. The numbers and arrangement of infraorbital foramina have been recorded, and their position relative to the orbital and alveolar margins defined by measurement in 205 gorillas, 178 chimpanzees, 82 orang-utans, 64 gibbons and 192 men of various ages.

2. In man there are, on an average, 1·05 infraorbital foramina in each maxilla; in the gibbon 1·2; in the gorilla 1·6; in the chimpanzee 2·4; and in the orang-utan 3·3.

3. In adult men and gibbons the distance between the infraorbital foramen and the orbital margin is about twenty per cent of that between the foramen and the alveolar margin. The corresponding figure for the gorilla is forty-five per cent, for the chimpanzee forty per cent and for the orang-utan thirty-five per cent.

4. The arrangement of the infraorbital apertures varies widely both within and between species.

5. While the milk teeth are erupting, the infraorbital foramen lies relatively nearer to the inferior orbital margin than in adults. In man, chimpanzee and gorilla, the adult position is reached by the time the first permanent molars are in line. In the orang-utan, the position of the foramen apparently continues to change until maturity is reached.

6. The numbers and arrangement of the infraorbital foramina are not correlated with the more obvious facial features (such as degree of prognathism), nor with variation in the basic subdivisions of the infraorbital nerve.

7. The position of the foramen relative to the orbital and alveolar margins is closely related to the degree of prognathism.

8. Although a single aperture appears to have occurred more frequently in the Australopithecinae than in the extant great apes, the foramen in these fossils lay in a position characteristic of the gorilla, and much further down the facial skeleton than in either modern man or the extinct species *Homo neanderthalensis*.

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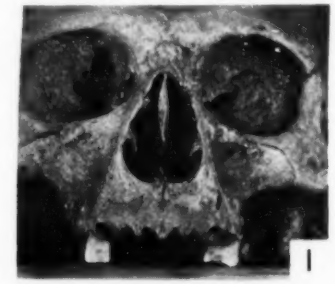
EXPLANATION OF PLATES

Plate 1

Figs. 1–3.—Variation in the infraorbital foramen of modern man.

„ 4–6.—Variation in the infraorbital foramen of the gibbon.



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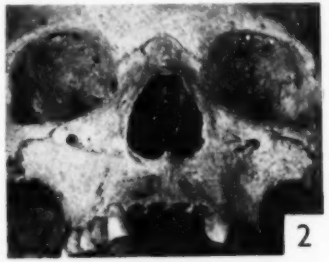

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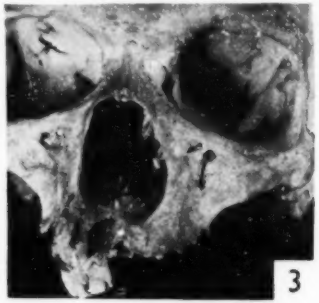

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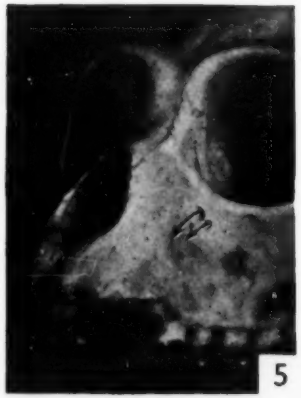

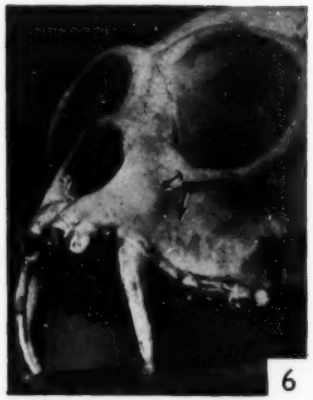

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Figs. 1—3 Variation in the infraorbital foramen of modern man

Figs. 4—6 Variation in the infraorbital foramen of the gibbon

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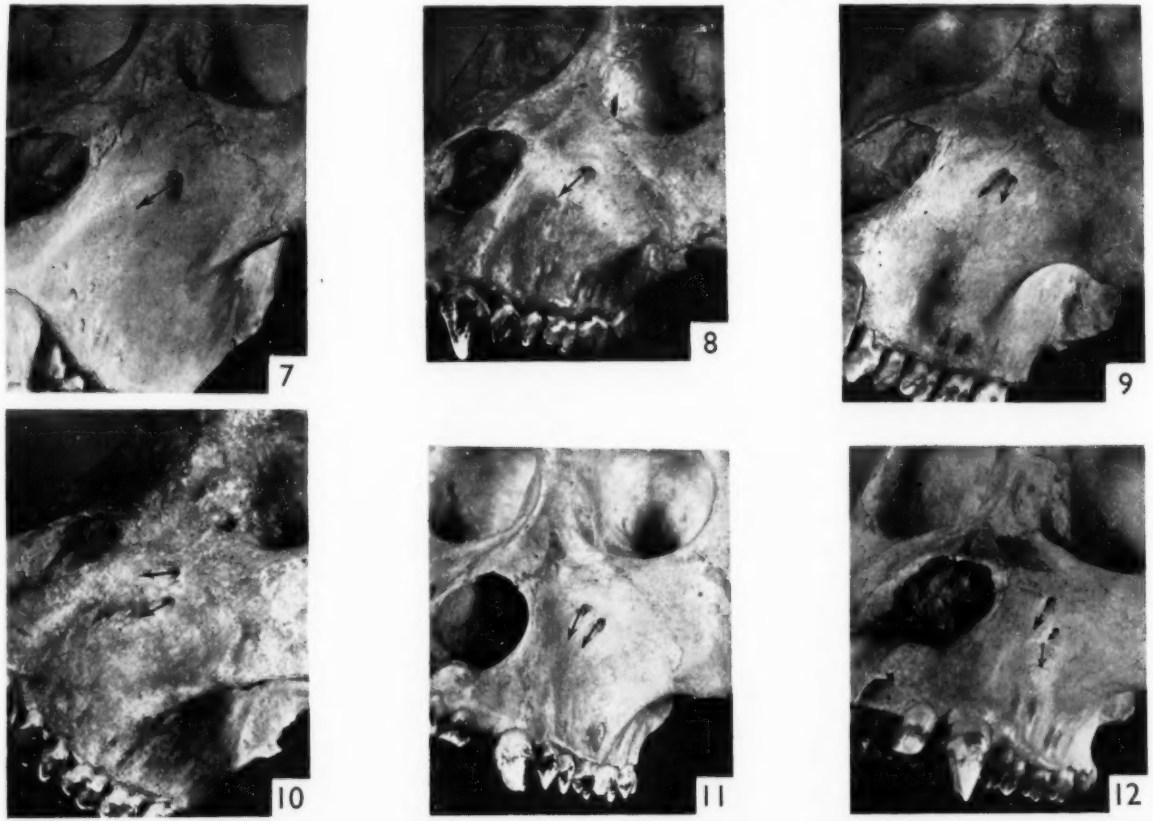

Figs. 7—12 Variation in the infraorbital foramen of the gorilla

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CHIMPANZEE

Figs. 13—18 Variation in the infraorbital foramen of the chimpanzee

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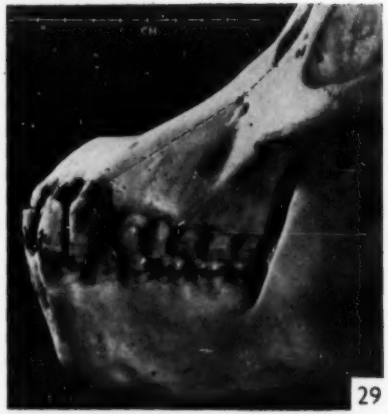
ORANG—UTAN

Figs. 19—24 Variation in the infraorbital foramen of the orang-utan

MAN

GIBBON



GORILLA CHIMPANZEE ORANG–UTAN

Figs. 25—29 Variation in the position of the infraorbital foramen in Hominoids

PLATE 2

Figs. 7–12.—Variation in the infraorbital foramen of the gorilla.

PLATE 3

Figs. 13–18.—Variation in the infraorbital foramen of the chimpanzee.

PLATE 4

Figs. 18–24.—Variation in the infraorbital foramen of the orang-utan.

PLATE 5

Figs. 25–29.—Variation in the position of the infraorbital foramen in Hominoids.

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LIST OF CONTENTS

Vol. 131

Part 3 (pp. 335–485)

Page

Ashton, E. H. & Oxnard, C. E.
Some variations in the maxillary nerve of Primates. (2 figures).... 457

Ashton, E. H. & Zuckerman, S.
The infraorbital foramen in the Hominoidea. (5 plates)..... 471

Crowcroft, Peter & Rowe, F. P.
The growth of confined colonies of the wild house-mouse (*Mus musculus* L.) : the effect of dispersal on female fecundity. (3 figures) 357

Elkan, E.
Further contributions on the buccal and pharyngeal mucous membrane in urodeles. (2 plates and 12 figures)..... 335

Marshall, N. B. & Thines, G. L.
Studies of the brain, sense organs and light sensitivity of a blind cave fish (*Typhlogarra widdowsoni*) from Iraq. (1 plate and 4 figures).... 441

Morris, B.
The yolk-sac of the mole *Talpa europaea*. (3 plates)..... 367

Morris, Desmond
The comparative ethology of grassfinches (Erythrurae) and mannikins (Amadinae). (5 plates) 389

Oxnard, C. E. See Ashton, E. H.

Rowe, F. P. See Crowcroft, Peter

Thines, G. L. See Marshall, N. B.

Zuckerman, S. See Ashton, E. H.

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"Proceedings" Vol. 131, Part 2, was published on 19th September, 1958.

Page
457
471
357
335
441
367
389
8.